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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 76, No. 6, pp. 385–406 NOVEMBER, 1949

HISTORY OF AN ESTUARINE BOG AT SECAUCUS, NEW JERSEY[1]

C. J. HEUSSER

Large parts of the Hackensack tidal marsh in northeastern New Jersey were covered with extensive forests of southern white cedar (*Chamaecyparis thyoides*[2]) for some time in the recent past. These forests contained trees of such size as are unknown today along the coast of New Jersey. Large stumps and logs are evident over much of the area as illustrated in

FIG. 1. Logs and stumps revealed by ditching at Secaucus. Area once covered by cedar forest is now covered with the reed, *Phragmites communis*.

figure 1. At a number of places, the forests have been succeeded by marshes, and the stumps and logs have been completely buried in marsh

[1] This study was supported by grants from the research council of Rutgers University.

[2] The nomenclature of Gray's Manual, 7th Ed. (Robinson and Fernald, 1908) is followed throughout.

[The Bulletin for September–October (76: 319–384) was issued August 24, 1949]

peat. Evidence of these forests can no longer be seen at the surface, but in some cases remains show up along ditches (fig. 2). Vermuele (1897), about the close of the last century, mapped this area and indicated the original outline of the cedar forests as well as the localities which at that time supported dense stands of living cedar.

FIG. 2. Ditching reveals remains of former cedar forest at Secaucus. Low tide aspect shows forest remains covered by marshland.

This paper represents a study of one of these former cedar bog forests and its associated marshlands at Secaucus, New Jersey. The problem was extended to include not only the disappearance of the white cedar forest and the subsequent invasion by the marsh, but also to trace the developmental history of the bog since the recession of the last of the Pleistocene ice. The investigations included a study of the present vegetation, the

underlying peat deposits, and the salinity of the tidal water. The Secaucus bog was chosen because of its position between two tidal creeks (fig. 3), namely Croma Kill and Mill Creek, and because its botanical history is so well known.

The Hackensack Valley in which the marsh is located occupies a portion of the Triassic plain of the piedmont of New Jersey. This valley is a broad lowland approximately 30 miles long, 5 miles wide at its southern end and about 2 miles wide at the north where it is crossed by the New

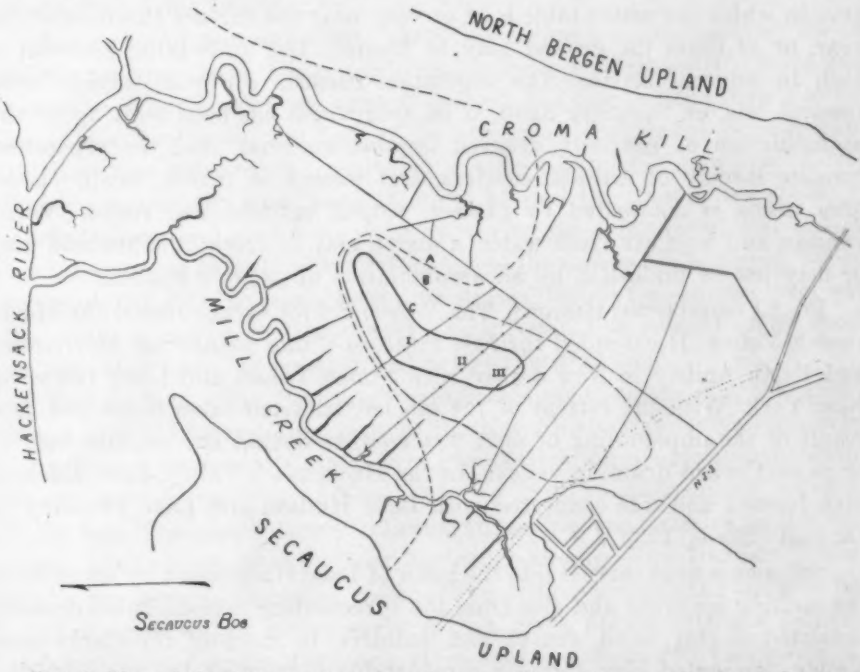

FIG. 3. Map of the Secaucus bog. Area between North Bergen upland and Secaucus upland is largely tidal marsh. South of the line made up of short dashes (A) to some extent beyond highway NJ-3 is the former area occupied by the cedar forest according to Vermeule (1897). The area within the long dash line (B) is covered with stumps and has been invaded by the marsh to line C. Line C represents the present extent of the bog. Lines I, II, and III refer to the respective north, middle, and south transects. Dots on these represent distances 100 meters apart. All other singly solid lines designate drainage ditches. New highway is shown in dotted lines.

York-New Jersey state line. On the east, the diabase sill of the Palisades forms a ridge, running parallel to the valley for its entire length. On the west, the Triassic shale and sandstone hills and the basaltic ridge known as the First Watchung form its western boundary. The lower end of the valley is today partly drowned by Newark Bay. Much more of it is occupied by an extensive area of tidal marsh and former cedar bogs extending to

about 10 miles north of Newark Bay. According to Vermuele (1897), at the beginning of this century, the marsh constituted an area of 20,045 acres, 1,465 acres of which were fresh meadow.

Since, as Waksman (1942) has pointed out, the terms swamp, bog, and marsh are loosely used, the following will clarify the usage as far as this paper is concerned. A swamp in the broad sense is a lowland community in which the ground is saturated with water for all or nearly all of the year. However, as considered here, more specifically, a swamp occupies an area in which the water table is at or very near the surface throughout the year, or at times the ground may be flooded. The underlying material is high in mineral matter. The vegetation consists of broad-leaved forest trees. A bog, on the other hand, is an area which has been built up by the accumulation of partially decayed organic material, and the vegetation consists largely of ericads, conifers, and mosses. A marsh, finally, is an area which is dominated by grasses, sedges, cattails, and rushes. While swamps and bogs are fresh water, a marsh may be fresh or saline and may or may not be underlain by an accumulation of organic remains.

POST-PLEISTOCENE HISTORY. The Wisconsin ice sheet covered the Hackensack Valley. It extended farthest south to a line connecting Morristown and Perth Amboy in New Jersey with Staten Island and Long Island in New York. With the retreat of the glacier, ice-front lakes developed as a result of the impounding of melt water either behind the moraine barrier or in northward draining valleys. In the Hackensack Valley, Lake Hackensack formed and was connected with Lake Hudson and Lake Flushing to the east (Reeds, 1933).

Sediments were carried into the basin of Lake Hackensack by water from the melting ice front and also from the surrounding region. These deposits consisted of clay, sand, gravel, and boulders. In much of the Hackensack Valley, laminated clay forms a considerable portion of the glacial drift. Reeds (1926, 1927) and Antevs (1922, 1928) have studied this varved clay at many places in the valley. Antevs (1928) concluded from his investigations that glacial Lake Hackensack existed for 2,500 to 3,000 years.

Although Salisbury (1902) considered Lake Hackensack connected with the sea in the form of a bay, Antevs (1922) contended that the area must have been a fresh water lake and not a bay of the sea. Antevs based this conclusion on the fact that the clays at Hackensack, New Jersey are distinctly varved. If the area had been covered by an arm of the sea shortly after the glacial lake formed, the clays would have been homogeneous for the most part, and only a few varves would have been distinguishable at the bottom. These bottom varves would then have comprised the only clay deposited under fresh water conditions. As a great number of varves were

deposited (more than 2,500 at Hackensack), Antevs (1922) further stated that the barrier damming the lake must have existed for a long time. The valley was depressed at the time the ice disappeared and was later uplifted. As the land was elevated (isostatic readjustment), the barrier damming the lake was obliterated. The terminal moraine may have acted as that barrier and if so would have been continuous during varve formation. If it were the barrier, there could have been no breaks where now Arthur Kill separates Perth Amboy from Staten Island and the Narrows separates Staten Island from Long Island.

According to Antevs (1928), while this region was depressed by the ice during the time Lake Hackensack was actively receiving drift sediments, the sea level was much lower than at present. His calculations show a lowering of sea level some 300 feet at the climax of the glacial period. Land which is now submerged constituted a wide coastal plain, which in New Jersey probably extended some 80 miles beyond the present sea shore. Of course the sea level must have come up during the existence of glacial Lake Hackensack due to melt water returning to the oceans. This rise of the sea was probably slow, so that a long time elapsed before the sea was level with the southern end of the Lake Hackensack basin. The present study would indicate that Lake Hackensack had drained by that time.

Recent Botanical History. During the nineteenth century, this area at Secaucus was known to botanists as the New Durham cedar swamp. When John Torrey wrote his "Catalogue of Plants Growing Spontaneously Within Thirty Miles of the City of New York" in 1819, he made special reference to the bog. The plants Torrey collected in the bog are included in this catalogue, labelled specifically "from the cedar swamp, New Durham." These plants are a valuable record inasmuch as they represent the natural flora of the bog during a rather early period. Such plants as *Calla palustris, Coptis trifolia, Cornus canadensis, Chiogenes hispidula,* and *Vaccinium oxycoccus* were found. Many of the plants possess a distinctly boreal affinity. Such plants as *Picea mariana* and *Larix laricina* reached their known southeasterly limit here.

Following Torrey's work, a period of over half a century elapsed before any further record of the flora of the bog is known to have been published. In 1881, Britton listed a number of plants which are not found in Torrey's catalogue. Shortly after, Britton published his "Catalogue of Plants Found in New Jersey" (Britton, 1889). In this work, a number of newly found plants were recorded. Many of the plants catalogued by Torrey persisted to this date. Especially to be noted in Britton's 1889 flora is the occurrence of *Picea mariana* and *Larix laricina.*

In 1919, Harshberger and Burns presented a study of the vegetation of

the Hackensack marsh, but no mention of growing white cedar is included. They appear not to have visited the Secaucus bog. By 1919, the cedar forests were probably largely destroyed. However, in April of 1949 about half a dozen trees of white cedar were found growing in a bog at Moonachie on the other side of the Hackensack River from Secaucus. In conversation with Mr. James L. Edwards of Montclair, New Jersey, the author learned that the last trees of white cedar in the Secaucus bog died about 1935.

In 1943, Waksman and co-workers investigated the peat underlying the bog. This is the most recent of the studies made in the area. It was not concerned with the individual kinds of plants present. The authors mapped the bog and the surrounding marsh and gave a rough description of the vegetation. They also constructed a peat profile showing the distribution of the kinds of peat.

METHODS

VEGETATION. For sampling the present vegetation of the Secaucus bog, the transect method was used. Three transects were laid out from Mill Creek on the northwest side of the bog to a wide drainage ditch on the southeast side (see map, figure 3). The transect lines were placed in such a way as not to cross the drainage ditches running into Mill Creek. In general, they were between 100 and 200 meters apart and from north to south were respectively named the "north," "middle," and "south" lines. This terminology is followed throughout the paper.

The middle transect was the longest. It ran approximately south 25° east from the bank of Mill Creek for a distance of 825 meters. The north line ran south 22° east for 803 meters, and the south line ran south 30° east for 795 meters. All lines were laid out with tape and compass, and stakes were placed 20 meters apart beginning with the initial stake at the bank of Mill Creek.

The object of the vegetational analysis was to obtain cover data. Cover was determined by the use of the numerical evaluation system of Braun-Blanquet (1932). For every 10 meter segment on all three transects, the cover of each species was estimated for the aestival and autumnal aspects. This was done at both seasons with tape and string using the 20 meter stakes as a guide.

SALINITY. For the determination of the salinity of the surface water, the method outlined by Denny (1927) was employed. Water samples were collected at every 20 meters on each transect during one period of incoming tide for the spring, summer, and fall. A further salinity study for comparative purposes was conducted approximately 30 miles south of Secaucus at Cheesequake marsh on Raritan Bay. This area was chosen because of the presence of a forest of living white cedar which grades into a brackish

marsh. On a transect running for a distance of 30 meters from within the forest out onto the marsh, water samples were taken at one meter intervals during one period of incoming tide in the summer and fall. All samples obtained in the field at Secaucus and at Cheesequake were brought back to the laboratory. Cover data for the white cedar and other forest plants as well as the marsh species were obtained along this transect.

The water samples collected at Cheesequake and Secaucus were taken on incoming tides on about the same date in the summer and fall, but the height of the tides was different at the two places for the different times of sampling. Sampling was done at Secaucus for the summer and fall on 21 July and 26 September 1948, respectively. From the "Tide Tables Atlantic Ocean for the Year 1948" (1947), the maximum height of the tide at Secaucus was found to have been about 4.9 feet and 4.4 feet for these respective dates. These figures are compared to maximum tidal heights of approximately 5.0 feet and 5.6 feet for 24 July and 24 September at Cheesequake marsh.

On the basis of the above information, there was a difference of only 0.1 foot between the maximum tidal heights at Secaucus and at Cheesequake for July. This little difference would thus allow salinity determinations comparable between these two places. However, the difference in the maximum tidal heights for September was 1.2 feet which precludes any comparison between the two places at that time.

PEAT. The peat was sampled by means of the Davis type American peat sampler. Stations were established 100 meters apart on all transects beginning with the initial stations at the bank of Mill Creek (dots on transect lines, fig. 3). Samples were obtained at one foot intervals at each 100 meter station to an approximate depth of 10 feet at which level gray clay was usually encountered. In all cases, sampling was done until the basement clay was reached. The peat from each level was examined in the field, and representative portions were brought back to the laboratory.

The purpose of the study was to construct profiles of the underlying peat along each transect. Field notes were used as the basis for these profiles. In the construction of the profile for the middle transect, laboratory data were used in addition to field notes. The peat from each level from stations 0, 100, 200, and 300 meters on the middle transect was examined in the laboratory under a binocular microscope at 15 ×. Fragments of the plant material, roots and rhizomes of herbaceous plants, small bits of wood, and fruits, were processed for identification by Benninghoff's (1947) technique. Identification of the wood was made through the use of the keys of Brown, Panshin, and Forsaith (1949) and Record (1934). In addition, slides of known species were compared. The herbaceous peat was identified by comparison with prepared slides of known species.

RESULTS

VEGETATION. The total number of species present in the bog and the surrounding marsh is 117. These are listed in table I. The cover for representative species on the middle transect is presented in figure 4. These data are essentially similar to those obtained from the north and south transects. They show the degree of dominance of the species and their distribution in space at two different seasons. For example, *Phragmites communis* and *Typha angustifolia* have both a broad distribution and a high degree of

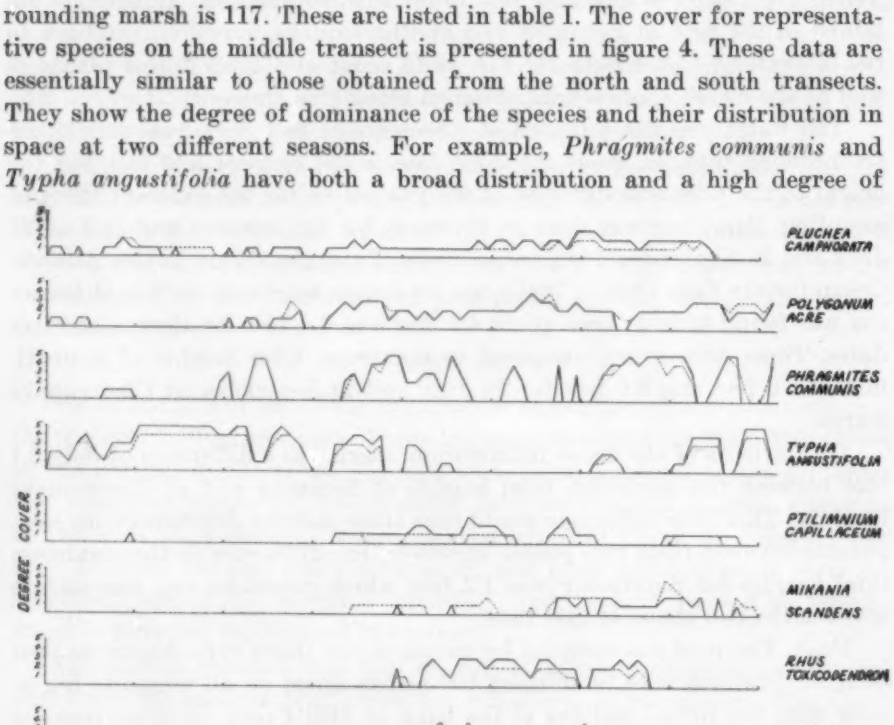

FIG. 4. Distribution and dominance of a few of the important species represented on the middle transect at Secaucus. Solid lines indicate results of summer sampling while the dotted lines those of fall sampling. Where only solid lines appear, there is indicated no change in the dominance and distribution of the species.

cover. *Scirpus olneyi,* on the other hand, has a high cover value where it occurs, but its distribution is more limited. Other plants such as *Typha latifolia* and *Rhus toxicodendron* occur only in the bog, while *Pluchea camphorata* and *Polygonum acre* are distributed for almost the entire length of the middle transect. These latter species have the widest distribution of all, occurring on approximately three-fourths of all the segments sampled. Also apparent is the great extent of *Phragmites communis* and *Typha angustifolia* (fig. 4).

TABLE I. *Plant list for the Secaucus bog and surrounding marshland for 1948. The order of plants follows that of Gray's Manual, 7th Ed. (Robinson and Fernald, 1908).*

Aspidium thelypteris	Rubus sp.
Onoclea sensibilis	Apios tuberosa
Osmunda cinnamomea	Rhus copallina
Osmunda regalis	Rhus toxicodendron
Typha angustifolia	Ilex verticillata
Typha latifolia	Acer rubrum
Alisma plantago-aquatica	Impatiens biflora
Sagittaria latifolia	Rhamnus frangula
Agrostis hyemalis	Psedera quinquefolia
Cinna arundinacea	Vitis labrusca
Distichlis spicata	Hibiscus moscheutos
Echinochloa walteri	Hibiscus oculiroseus
Glyceria nervata	Hypericum virginicum
Panicum virgatum	Viola pallens
Phragmites communis	Lythrum salicaria
Spartina cynosuroides	Cicuta maculata
Spartina glabra var. pilosa	Ptilimnium capillaceum
Spartina michauxiana	Sium cicutaefolium
Spartina patens	Nyssa sylvatica
Zizania aquatica	Clethra alnifolia
Cyperus nuttallii	Gaylussacia frondosa
Cyperus strigosus	Leucothoe racemosa
Eleocharis palustris	Rhododendron viscosum
Scirpus americanus	Vaccinium atrococcum
Scirpus olneyi	Vaccinium corymbosum
Scirpus robustus	Vaccinium corymbosum var. amoenum
Scirpus validus	Lysimachia thyrsiflora
Peltandra virginica	Asclepias incarnata var. pulchra
Lemna minor	Convolvulus sepium
Juncus gerardi	Cuscuta compacta
Hemerocallis fulva	Verbena hastata
Maianthemum canadense	Lycopus uniflora
Smilax rotundifolia	Scutellaria galericulata
Iris versicolor	Solanum dulcamara
Betula populifolia	Sambucus canadensis
Quercus bicolor	Viburnum dentatum
Quercus palustris	Viburnum nudum
Quercus rubra	Viburnum prunifolium
Boehmeria cylindrica	Ambrosia artemisiifolia
Pilea pumila	Aster novi-belgii
Polygonum acre	Aster subulatus
Polygonum arifolium	Baccharis halimifolia
Polygonum hydropiperoides	Bidens connata
Polygonum muhlenbergii	Bidens laevis
Polygonum sagittatum	Bidens trichosperma
Polygonum scandens	Erechtites hieracifolia
Rumex britannica	Eupatorium perfoliatum
Atriplex patula	Eupatorium purpureum
Acnida cannabina	Gnaphalium polycephalum
Phytolacca decandra	Helianthus giganteus
Caltha palustris	Mikania scandens
Ranunculus sceleratus	Pluchea camphorata
Thalictrum polygamum	Solidago elliottii
Radicula nasturtium-aquaticum	Solidago graminifolia
Radicula palustris var. hispida	Solidago rugosa
Amelanchier oblongifolia	Solidago scabra
Pyrus arbutifolia var. atropurpurea	Solidago sempervirens
Prunus serotina	Solidago serotina
Rosa carolina	

Seasonal aspect is important in the study of the bog and marsh vegetation. *Ptilimnium capillaceum* and *Mikania scandens*, although well distributed, vary as to the time they reach their maximum cover, *Ptilimnium* reaching its peak of development during the summer, *Mikania* in the early autumn. It was because of this change of seasonal aspect that the two periods of study were undertaken. The members of the Compositae, for further example, were apparent during the summer, but it was during the fall sampling that they became important. Of interest with regard to *Mikania* is its frequent ability to spread over large areas of *Phragmites*, bending them down to about waist height.

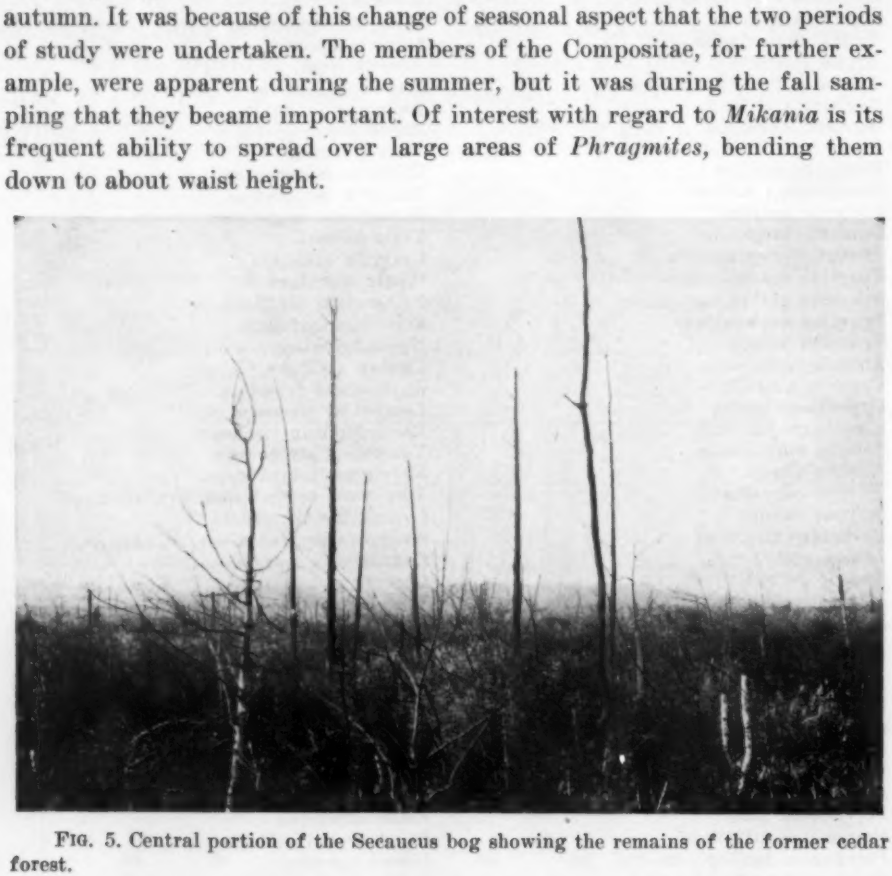

FIG. 5. Central portion of the Secaucus bog showing the remains of the former cedar forest.

Zonation is apparent in the distribution of plants surrounding the central portion of the former cedar bog. Figure 4 shows this in both the dominance and distribution of the plants. The species of *Spartina* are found along Mill Creek. *S. cynosuroides* occurs as far back from the bank as 70 meters (average about 30 meters), while *S. michauxiana* extends to about 20 meters, and *S. glabra* var. *pilosa* is found only on the immediate bank. This group along with sparse patches of *Juncus gerardi* occupy the area of greatest salt concentration. Behind this, *Typha angustifolia* and *Scirpus olneyi* make up a zone approximately 250 meters broad. These species vary in dominance, often occurring mixed or separate, with *Typha* having a

greater cover and more continuous distribution than *Scirpus*. Near the *Spartina* zone, *Scirpus olneyi* is often mixed with small amounts of *Scirpus americanus*. Back from the *Typha-Scirpus* zone, *Scirpus olneyi* forms an almost pure belt about 30 meters wide which then gives way to a preponderance of *Phragmites communis*. The *Phragmites* zone immediately surrounds the central area of the bog. In many places in the bog, *Phragmites* now forms small colonies. These have undoubtedly developed since the disappearance of the forest. *Phragmites* also occurs in colonies throughout the marsh.

Figure 5 shows the condition of the remains of the former white cedar forest. This remnant of the former, more extensive forest today measures roughly 1000 by 150 meters and is a dense entanglement of shrubs and small trees, both living and dead. The living vegetation is partly made up of the woody plants *Rhododendron viscosum, Clethra alnifolia, Vaccinium* spp., *Amelanchier oblongifolia, Rhamnus frangula,* and *Ilex verticillata.* Both dead and young living trees of *Nyssa sylvatica, Quercus bicolor, Acer rubrum,* and *Betula populifolia* are scattered among the shrubs. The predominant herb species are *Pluchea camphorata, Polygonum acre,* and *Ptilimnium capillaceum.*

The results of the study at Cheesequake marsh reveal the cedar forest to be made up of *Chamaecyparis thyoides* with *Acer rubrum* of secondary importance. Along the transect, the cedars were all found to be small trees. They grade for the most part from individuals only slightly greater than 1 inch d.b.h. (diameter breast high) to small saplings where the edge of the forest makes contact with the marsh. The largest trees on the transect are 5 inches d.b.h. Seedlings of white cedar are fairly well dispersed throughout the forest and are scattered beyond the margin of the forest on the marsh. A few small saplings are growing beyond the limit of the occurrence of seedlings.

In the cedar forest, *Vaccinium corymbosum, Ilex verticillata, Rhododendron viscosum, Clethra alnifolia,* and *Magnolia virginiana* are scattered throughout. As the forest becomes lower in stature on meeting with the marsh, the canopy opens and such plants as *Osmunda regalis, Vaccinium macrocarpon, Sanguisorba canadensis, Rhus toxicodendron,* and *Cladium mariscoides* are found along with the white cedar and red maple. On the adjacent part of the marsh, the vegetation consists predominantly of *Cladium mariscoides* with lesser amounts of *Panicum virgatum.* Although the marsh continues for 150 meters beyond the transect before Cheesequake Creek is reached, the study was terminated at 30 meters due to the presence of an artificial drainage ditch. The greater part of the marsh beyond the ditch consists of *Spartina patens, Distichlis spicata, Eleocharis rostellata,* and *Scirpus americanus.*

SALINITY. The results of the salinity determinations for the middle transect at Secaucus, expressed in both per cent of sea water and parts per thousand of chlorides, are given in figure 6. The curves for the salinities on the three transects for spring, summer, and fall show a similar trend. On all the curves there is a distinct increase in salinity for the summer and fall over that of the spring. For example, the salinities in the marsh for the spring determination at 300 meters from Mill Creek on the north, middle, and south lines respectively were 5.80, 4.80, and 6.10 per cent sea water. At the same stations in the summer, they were 8.60, 7.35, and 8.40 per cent; and for the fall, the results were 23.50, 20.35, and 20.10 per cent. The salinities for the spring at points within the bog 500 meters from Mill Creek likewise on the north, middle, and south lines respectively were 4.30, 4.55,

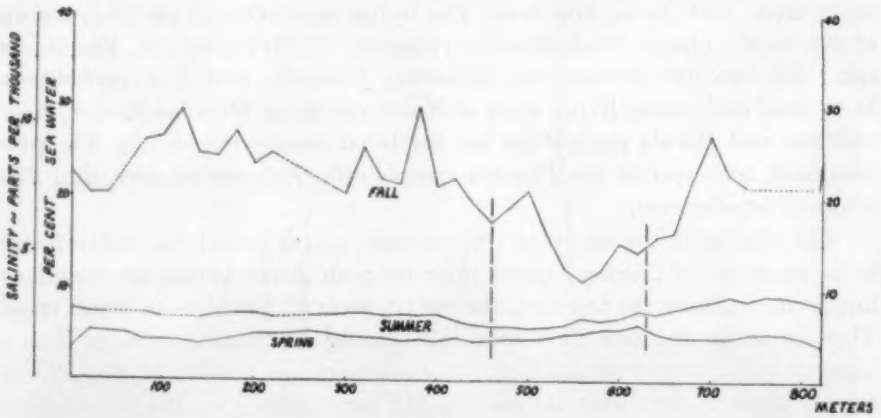

FIG. 6. Salinity curves for the middle transect at Secaucus for the spring, summer, and fall sampling. Irregularities in the fall curve are due to high evaporation and extremely low rainfall following a neap tide. Dotted lines indicate no sample determination at the particular station. Upright dash lines set off the open portion of the bog.

and 5.10 per cent sea water. At the same stations for the summer, they were 5.80, 5.80, and 6.95 per cent and for the fall 14.15, 20.75, and 14.90 per cent. The curves for the spring and summer on all the transects are rather smooth and show no pronounced irregularity while those for the fall show marked irregularity. Especially significant, as illustrated in figure 6, are the lower salinities in the open bog (area between broken lines in figure 6) and the area immediately on either side. Although these lower salinities are not striking on the spring and summer curves, the fall curves show this very well in the low dip that occurs as the bog is reached.

Although spring salinities were not determined at Cheesequake marsh, the results of the summer and fall sampling show an increase in fall salinity over that of summer similar to that found at Secaucus. At a point on the

marsh 6 meters out from the last cedar sapling, the salinity reached 7.55 per cent sea water in July. This was the highest salinity on the transect at that time. In September, the salinity at this same point reached 34.20 per cent sea water which was nearly the highest recorded at that date. The maximum salinity in the vicinity of the growing cedar was 2.60 per cent during the time of the summer study. During the fall the maximum had greatly increased to 28.10 per cent.

A comparison between the minimum salinities recorded during the summer in the former cedar bog at Secaucus and the maximum salinity determined in the vicinity of the living cedar at Cheesequake at the same time, reveals a higher salinity at Secaucus. While in the Secaucus bog on the north, middle, and south transects respectively, minimum salinities in July were recorded at 5.10, 5.80, and 6.90 per cent sea water, at Cheesequake the maximum salinity for the living cedar at that time was 2.60 per cent. This maximum salinity of 2.60 per cent is even lower than the minima recorded in the cedar bog at Secaucus for the spring: 3.90, 4.40, and 4.90 per cent on the respective north, middle, and south lines. The salinity at Cheesequake during the spring, although not studied, was probably less than 2.60 per cent.

It is interesting to note that during the time of the fall determinations, the minimum salinities in the Secaucus bog were below rather than above the maximum salinity beneath the growing cedar at Cheesequake. At Secaucus, the minimum salinities recorded during the fall on the north, middle, and south lines respectively were 12.30, 11.00, and 12.35 per cent sea water. At Cheesequake in the vicinity of the living cedar, the maximum salinity at any time was 28.10 per cent. In other words, cedar is growing at Cheesequake where occasionally it is subjected to tidal water which is highly saline. In the above case, the water was even more highly saline than in the Secaucus bog where the cedar is no longer growing. As mentioned earlier, however, it was a higher tide at Cheesequake than at Secaucus at the time the fall determinations were made.

Precipitation data kindly furnished by the U. S. Department of Commerce Weather Bureau at Newark, New Jersey (about six miles southwest of Secaucus and about twenty-five miles northwest of Cheesequake) show that monthly precipitation totals were approximately similar during June and July (the time at which the spring and summer sampling was done) with 6.19 and 6.88 inches, respectively. In September, at which time the salinities had greatly increased, the precipitation for the month reached a low for the year at 1.14 inches. This information is significant in showing the relationship between the precipitation and the salinity data.

PEAT. The peat in the profile for the middle transect consists for the

most part of two main types: marsh peat and forest peat (fig. 7). Marsh peat forms a layer for approximately 300 meters in from Mill Creek, overlying forest peat. It is deep at the creek and thins out gradually becoming merely a superficial layer as the bog is approached. Marsh peat also overlies forest peat on the east side of the bog.

The marsh peat is almost everywhere a black, well-consolidated, highly organic material, made up largely of *Scirpus olneyi* mixed at some levels with *Juncus gerardi* and at others with *Typha angustifolia*. At Mill Creek, there is a deposit of silt extending to a depth of 8 feet. This silt occurs as a superficial layer over much of the marsh back from the creek (specifically the area above the broken and dotted line in figure 7). Some reed peat made

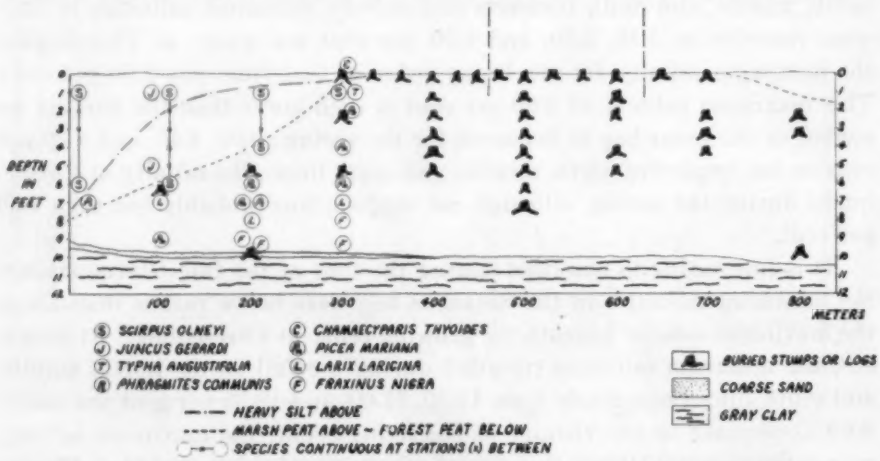

FIG. 7. Peat profile for the middle transect at Secaucus. Although not shown, angiospermous peat occurs at the bottom at stations 0 and 100 as well as 200 and 300 meters. Upright dash lines set off the open portion of the bog.

up of rhizomes of *Phragmites communis* is found at 7 feet at stations 0 and 200 meters.

Forest peat forms the bulk of the underlying plant remains for the middle transect (fig. 7). Within the area of the present bog and to some extent on either side, this type of peat is continuous from the bottom of the profile to the top. However, beyond this, it becomes overlain by an increasing depth of marsh peat. By and large, the forest peat is soupy, poorly consolidated, and colored a reddish-brown which is generally characteristic of coniferous peat.

Peat was analyzed at stations 0, 100, 200, and 300 meters on the middle transect. At station 300 meters which is the only station of the four analyzed where woody remains extend from bottom to top, there is an apparent gradation and layering of species in the vertical profile. The bottom layer

directly above the sand and clay consists for the most part of angiospermous woody plants with *Fraxinus nigra* especially evident. This layer is about 2½ feet in thickness with a darker color and is well-consolidated in contrast to the upper layers. From the 7 foot level to about 2 feet, *Picea mariana* and *Larix laricina* appear to be mixed. Stumps of *Chamaecyparis thyoides* are found at the surface. Marsh peat has accumulated about 6 inches deep about the bases of these stumps, so that they are partly buried.

The angiospermous peat layer is continuous over the bottom at the four stations studied. The *Picea-Larix* layer thins out as Mill Creek is approached and finally ends at station 100 meters. *Picea* and *Larix* were difficult to identify. At stations 200 and 300 meters, at 8 and 7 feet, respectively, cones of *Larix* and spur shoots characteristic of *Larix* were observed in the peat. The identification of the wood found at these levels as *Larix* was thus strengthened by this evidence.

Throughout the woody peat, regardless of the consolidation of the material, stumps and logs are buried at nearly all depths. At some stations, especially those within the bog itself, sampling was difficult due to the extensive occurrence of buried tree trunks. Although the profiles of the north and south transects are not presented, they illustrate the stratification of stumps and logs and also the overriding of the marsh peat upon the forest peat.

The basement material beneath the bog is gray consolidated clay. Variable amounts of sand are found above the clay, especially near Mill Creek. From information kindly given by the New Jersey State Highway Department for a sampling station near the fork in route N J–3 east of Secaucus (fig. 3), it was learned that the underlying material consists of gray clay to a depth of about 18 feet, soft brown clay to a depth of approximately 57 feet, and soft reddish clay with some pebbles to 102 feet. At this level sampling was discontinued.

The road building operations of the N. J. State Highway Department through the southern end of the former cedar bog are of interest in regard to the peat deposit (road in dotted lines in figure 3). The author has called attention to the large logs and stumps which were removed during these operations (Heusser, 1949).

DISCUSSION

The developmental history of the Secaucus bog has been greatly influenced by glacial activity and especially by the post-Wisconsin rise in sea level. In the peat underlying the bog, the remains of forests which formerly covered the area are evident. These forests became preserved as a result of the rise of the sea. In the Secaucus bog, this is clearly recorded in the gradual spread of the marsh deposits at the expense of the forest peat.

Long before glacial Lake Hackensack drained, the sea level had been

rising as a consequence of the increase of melt water returning to the oceans. This rise has been irregular throughout, caused by minor fluctuations in the ice during deglaciation and isostatic readjustment (Flint, 1947; Marmer, 1948). Some time during the period that the sea was coming up, the bed of glacial Lake Hackensack was uplifted, tilted and the lake drained. The clay and sand, deposited in the lake basin as the glacier retreated, were thereby exposed. The lake bed was thus free to receive the initial waves of invading plants. As the exposed basin was flat and probably poorly drained, only those species capable of growing under such conditions migrated into the area.

In the vicinity of Secaucus, it appears that *Fraxinus nigra* was among the first major forest species to have left a record. This is shown in the peat profile for the middle transect. It is unknown whether or not any forests preceded this black ash swamp. Conifer forests consisting possibly of fir may have existed prior to the ash, but no record of such forests was evident at Secaucus. The forest record only began when conditions became favorable for peat formation.

It is unknown how long the black ash swamp existed at Secaucus. After it was invaded by *Picea mariana* and *Larix laricina*, *Fraxinus nigra* persisted for a time mixed with larch and black spruce, but was ultimately succeeded by the latter two species which were favored by the rising water table. It is of interest to note that at Budd Lake, New Jersey, about 40 miles west of Secaucus, the converse of the above succession is occurring where black ash is slowly growing out on to a mat occupied by larch and black spruce, as the per cent of minerals in the peat increases. The above is a typical upland northern bog succession, but this situation reverses in an estuarine bog on a submerging coast as at Secaucus.

In interpreting this succession from a hardwood forest to one of larch and spruce, the change in the level of the water table must be taken into consideration. As the sea entered the southern end of the basin, the water table was raised. With continued encroachment of the land by the sea, the water table continued to rise higher and higher. Bartlett (1909) has called attention to this condition in his study of the *Chamaecyparis* bog at Woods Hole, Massachusetts. Black ash could not persist when the water table became critically high and raw peat began to accumulate rapidly. With the increase in the height of the water table, rapid peat formation was made possible and black spruce and larch with their associated vegetation invaded.

The dominance of *Picea* and *Larix* continued for a long time. With the persistent rise of the water table as the sea level came up, the bog grew upward. Only those species capable of living under such conditions could remain. Larch and black spruce were able to withstand the perpetuation of

these conditions. Their persistence up to the end of the nineteenth century is evidence of this.

Evidence of the continued increase of sea level is found in (1) the superposition of stumps and logs in the profiles, (2) the phenomenon of marsh peat overriding forest peat, and (3) the amount of silt carried over the marsh bordering the bog. The trees as they died were buried by the peat as the sea level came up. Marsh peat has impinged upon the forest as a consequence of increased tidal flooding from Mill Creek on the west and Croma Kill on the east. As the tides penetrated further into the bog, silt deposition in the peat was likewise coincident with the extent of the tidal flooding.

The entrance of brackish water into the area on the west side of the bog is not entirely evident until some time after the development of the spruce-larch forest. At station 0 meters on the middle transect at the bank of Mill Creek (fig. 10), the brackish water indicator plant, *Scirpus olneyi*, first appears in the profile at the 6 foot level. At 4 and 5 feet above, occurs a deposit of silt which does not contain plant remains. This is indicative of a certain amount of shifting in the channel bed in the coarse of centuries.

Since the first presence of brackish water in the Secaucus area, the rise of the sea level, as indicated by the marsh peat in the profile for the middle transect, has been essentially continuous. The effect of the sea rise is best shown on the west side of the bog where the gradient of marsh peat overlying forest peat is steeper than on the east. This is due to the fact that the bog is nearer Mill Creek than Croma Kill (see fig. 3), and the tides are consequently more effective from Mill Creek.

In the profile for the middle transect, *Chamaecyparis thyoides* is found only at or near the surface. As no remains of white cedar are evident except at or near the surface, one is lead to conclude that this species migrated into the Secaucus bog rather recently after a long period of spruce-larch dominance. According to Torrey (1819), at the beginning of the nineteenth century: "The cedar swamp . . . is entirely overgrown with the *Cupressus thyoides* or white cedar, and other evergreens." The coniferous forest at that time appears to have consisted largely of cedar in which larch and black spruce were less abundant. White cedar, possessing a more austral affinity, presumably migrated up the coastal plain from a southern distribution center, following a long time after the spruce-larch immigration.

The profile Waksman and his co-workers (1943) present for the bog is based upon a generalized classification of the types of peat rather than specific plant remains. They show buried "stumps" and forest peat and overlying marsh peat. What is labelled *"Carex"* peat type is presumed to be *Scirpus* peat. The portion of the profile designated as "water" was not found by the author. Possibly they refer to soupy peat which, however, was

found underlying practically the entire bog portion and even parts of the surrounding marsh. Also, the material designated as "clay" and shown below the bog and up to the surface on the borders is not the same material throughout. Rather, what underlies the bog is consolidated gray clay of glacial origin. The material shown bordering the bog is heavy silt brought in during the rise of sea level.

Since early times when the first settlers occupied the Hackensack area, the cedar forests were exploited for such purposes as ship building and road building. Van Winkle (1924) tells of the early laying of corduroy roads from split cedar logs. One such road was built by John Schuyler as early as 1759. Van Winkle also mentions the cedar forests as a source of Christmas greens which were no doubt cedar and spruce.

This exploitation must have damaged these forests, but the destruction done by fire, mosquito ditching, and dyking was far more effective. As far back as the beginning of the eighteenth century, fire is known to have ravaged the Hackensack area (Van Winkle, 1924). In fact at that particular time, the area was purposely burned to force pirates and robbers from hiding in the cedar forests. Since then, the frequency of fire has gradually increased, so that today fire is a very common occurrence in the region especially in the fall and early spring.

Much of the area was formerly cut for "salt grass" (*Spartina patens* and *Distichlis spicata*) and "three square" (*Scirpus olneyi*). This cutting seemed, incidentally, to prevent fire, as the stubble that was left was not much of a fire hazard. The salt grass was used a great deal as bedding for horses, but with the advent of the automobile, the horse disappeared and likewise, the cutting on the marsh gradually stopped. Fires which then started, burned through extensive areas without being checked. Largely as a consequence of the increase of fire, the cedar forests were eventually destroyed.

Ditching has been exceedingly important in changing the drainage pattern and thus greatly effecting this distribution of salt and fresh water. Vermeule (1897) showed the distribution of artificial drainage ditches already constructed in 1896. Bog areas beyond the tide fed by run-off from the upland, springs, and by rainfall were thereby more rapidly drained while outer margins received greater influence of tidal flooding. The cedar forests were thus affected in the course of the ditching due to a greater influx of saline water. In some cases, dyking caused a lowering of the water table to such a critical point, that the drier conditions resulting led to an accentuated ravaging of the forests by fire.

About the beginning of the 1930's, the Secaucus bog was further ditched as a measure of mosquito control. Figure 3 shows the location of the ditches

as well as the effect of ditching on the extent of the bog portion. The area within the solid line which represents the open portion of the bog was not ditched. This bog area was formerly continuous with the upland to the southwest, but after ditching, the ditched area was invaded and covered with *Phragmites communis*. The run-off of fresh water from the upland is partially cut by these ditches, and the existence of the open bog depends a great deal on rainfall. Ditching may have contributed to the death of the last cedars about 1935.

Although fire and the influx of brackish water are largely responsible for the condition of the Secaucus bog, there are a number of associated factors which are also responsible and should be mentioned. Since the turn of the last century, the Hackensack area has become increasingly industrialized. Industrial wastes have been dumped into the creeks and have had much to do with the changing vegetation at Secaucus. The water in Mill Creek has been polluted by the discharge of sewage effluent from the Secaucus disposal plant. Correspondingly, Croma Kill receives the discharges of the disposal plant in North Bergen. Pollution has not only affected the river system, but the air has also been polluted by smoke and poisonous industrial gases. Such conditions have undoubtedly added to the difficulties of existence for cedar. There is also the factor of the amount of fresh water flow in the Hackensack River. This has been reduced as a result of the increase in the use of water by the metropolitan region. This increased utilization of fresh water has resulted in saline tides reaching further up the river. The widening and deepening of the channel of the river has in recent years also allowed for increased flooding by the tides. As a result of the changes brought about by these factors, the plants in the Secaucus bog present today are quite different from those recorded by Torrey in 1819. Only a few of the former bog plants yet remain, and if the present tendency continues these will soon disappear.

Regarding the possibility of cedar again growing in the bog, it seems improbable that it could be able to develop under the present brackish conditions, even barring fire. This is based upon a reference to the salinity of the water in the vicinity of growing cedar in the Cheesequake forest. The evidence obtained in this study is addmittedly meager, but is suggestive of long periods of too high salinity at Secaucus. This is related to increased tidal effects and decreased source of fresh water from the nearby upland, both resulting from ditching and decreased flow of fresh water in the Hackensack River. It is also tied up with increased invasion by salt water due to coastal submergence. One is lead to doubt that cedar could exist at the present time under such conditions. However, whether or not it could exist actually requires further study than is presented here.

Coastal submergence has and continues to be a factor of prime importance in the dynamics of this bog. The formation of peat in the bog and in the surrounding marsh is due to rising sea level resulting from the relative change in the level of the land and sea. Marmer (1948) states that this change has been occurring on the Atlantic coast of the United States at about 0.02 foot a year since 1930 and at about one seventh of that rate during a 35 year period prior to that time. If this rise in sea level continues, the bog at Secaucus will eventually be covered by marsh peat. This ultimate condition seems inevitable in the light of past geological history, even aside from the factors induced by human interference.

SUMMARY

1. A study of a former southern white cedar bog at Secaucus, New Jersey in the Hackensack tidal marsh is presented. The object of this study was to trace the post-Pleistocene history of the bog and also, to learn what factors have acted to destroy the forest.

2. In gaining this end, an investigation was made of the vegetation, the water salinity, and the underlying peat. As a basis for these studies, three transects were run through the bog and the surrounding marshland. At Cheesequake marsh, 30 miles south of Secaucus on Raritan Bay, another transect was run to study the condition of saline tidal water in relation to a thriving forest of white cedar.

3. Zonation is evident in the marsh vegetation surrounding the bog at Secaucus. *Spartina, Typha angustifolia-Scirpus olneyi, Scirpus olneyi,* and *Phragmites* zones are present. The vegetation of the bog consists of shrubs and scattered deciduous trees, both living and dead, and herbs which have invaded as a result of fire opening up the community and an increased salinity of the water of the bog. Few of the original plants remain.

4. Results of the salinity tests are not conclusive, but suggest that salinity may be a factor in the elimination of cedar from Secaucus.

5. Peat profiles for the three transects show the influence of a rising sea level on the size of the bog. The relative distribution of marsh and forest peat in the profiles indicates an increasingly more limited extent of the bog at higher levels. Forest peat has been and is being overridden by marsh peat. An angiospermous peat layer is evident at the bottom of the profile. Above this, gymnospermous plant remains are present.

6. The post-glacial history is discussed. Following the recession of the ice, glacial Lake Hackensack covered the area. As the land was uplifted, the lake was drained, and the bottom exposed to invading plants. The peat profile reveals *Fraxinus nigra* as one of the first forest species preserved. This species did not persist due to the rise in sea level, but was succeeded by

Larix laricina and *Picea mariana* which were favored by the rising water table. These species persisted to the close of the nineteenth century. *Chamaecyparis thyoides* more recently migrated into the bog.

7. The present day vegetation in the bog is quite different from that described by Torrey in 1819. Ditching and fire are the two major factors which have brought about the rapid decadence of the cedar forest today. The rise of sea level has throughout the history of the bog gradually reduced the size of the bog forest. Aside from human interference, it appears that the ultimate fate of the bog is burial in marsh peat.

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THE THREE SUBSPECIES OF ARISAEMA TRIPHYLLUM

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The purpose of the present brief discussion is to validate, explain and make available to other workers three subspecific names which the writer has used in his unpublished manuscript[1] on *Arisaema* in temperate North America.

After considering the problem of the classification of the American jack-in-the-pulpits from the morphological, ecological and cytological points of view, the author has decided that three populations exist and that these should be treated as subspecies of a single species, namely *A. triphyllum*.

A. TRIPHYLLUM subsp. **triphyllum** Huttleston, subsp. nov., based on *Arum triphyllum* L. Sp. Pl. ed. 1. 965. 1753.

Plants with veins of scapes and leaf-sheaths usually not prominent; leaves broad, glaucous beneath; lateral leaflets oblique at bases and moderately to strongly gibbous on outer margins, acutely or obtusely angled at bases; spathe-tubes smooth or obscurely fluted with broad, 2–7 mm., flanges at tops; insides of laminae from wholly green to wholly purple, but usually purple with more or less broad stripes of green or whitish to the tips; growing in dry to moist, shaded locations; somatic chromosome numbers 28 and 56. (The author has made chromosome counts for about 50 plants from various parts of the range. These counts were 2n = 56 with the exception of those for two plants collected at Big Gully, Cayuga County, New York, which had 2n = 28. These latter plants could not be separated morphologically from the others.)

Range: In eastern North America from the Gaspé Peninsula and northern Minnesota south to southern Florida and eastern Texas and west to eastern Texas and western Minnesota.

Until recently most botanists thought that this was the variation that Linnaeus had when he described *Arum triphyllum* in his *Species plantarum*. In 1940, Fernald in *Rhodora* stated and gave evidence to support the view that Linnaeus did not have this plant but had what the present writer calls *A. triphyllum* subsp. *pusillum*. After carefully reviewing the evidence, the present author cannot agree with Fernald's conclusion. The specimen in Linnaeus' herbarium which he had marked "4 triphyllum" is definitely a member of this species, but it cannot be assigned to a subspecies since distinguishing characters are not evident. The present writer has not seen the specimen, but a photograph of it appears in *Rhodora* **42**: *pl. 298*. The lateral leaflets are moderately oblique at the bases and the spathe-lamina is pale.

[1] Huttleston, D. G. 1948. A Taxonomic Study of the Genus *Arisaema* in North America. Dissertation, Cornell University.

These are characteristics common to both variations in question. True, the spathe-lamina is narrowly ovate, a condition which, although more common in subsp. *pusillum*, is not infrequent in subsp. *triphyllum*. The flange at the summit of the spathe-tube appears to be rather broad, which is certainly more indicative of the typical subspecies.

In his description, Linnaeus listed three varieties. After a brief description, he designated two other variants beta and gamma. We must assume that the first description alone refers to the typical variant. After this description, which is far too brief for identification, Linnaeus listed four references; Gronovius's *Flora Virginica*, p. 113, Bauhin's *Pinax*, p. 195, *Prodromus*, p. 101, and Dodart's *Memoirs*, p. 81. The first citation, that of Gronovius, reads as follows:

> Arum acaule, folio ternato.
> Arum minus triphyllum i. Arisarum pene viride Virginianum. Mor. Hist. Oxon. Part III. S. XIII, p. 547. n. 44. T. 5. f. 43.
> Arisarum triphyllum, pene viride, Banist. Clayt. n. 66.

Since Linnaeus cited the Morrison reference under his variety beta, the only basis that is found in this reference is "Arum acaule, folio ternato." which is unidentifiable.

The author, then, must go to the second reference given by Linnaeus. That is Bauhin's *Pinax*, p. 195, and *Prodromus*, p. 101. On page 195 of the *Pinax* is found a very diagrammatic sketch which can be assigned to the species, but not to a subspecies. On page 101 of the *Prodromus*, however, one finds a description which is sufficiently complete to assign it to a subspecies. In the first place, although Bauhin stated that the specimen came from Toupinamboult, Brazil, the plant was actually collected in Canada where subsp. *pusillum* does not grow.[2] In the second place, Bauhin stated that his plant had whitish-green leaves which would indicate glaucescence and the two outer leaflets had a sinus between them on the lower side which would indicate a gibbous condition. Lastly, he stated that the spathe was dark red with whitish stripes through the center. These are all characters of subsp. *triphyllum* as it is here conceived. The fact that the spadix was stated to have been bifid at the summit is not important since plants are occasionally found with compressed and sulcate or even divided spadices.

The last citation given by Linnaeus, that of Dodart's *Memoirs*, p. 81, is even more certainly subsp. *triphyllum*, since he provided an excellent illustration of this subspecies and stated in the description that the leaves were whitish underneath.

A. TRIPHYLLUM subsp. **pusillum** Huttleston, comb. nov., based on *A. triphyllum* var. *pusillum* Peck, Rep. N. Y. State Mus. **51**: 297, 298. 1899.

[2] Juel, H. O., 1923. Nova Acta Soc. Sci. Upsal. IV. 5: 69–70; and Juel, H. O., 1931. Rhodora 33: 175.

Plants with veins of scapes and leaf-sheaths not prominent; leaves light green, but never glaucous, beneath; lateral leaflets moderately to slightly oblique on outer margins and acutely angled at bases; spathe-tubes smooth with flanges 1–2 mm. broad at tops; laminae wholly purple or wholly green, when purple, rarely finely striped with green above the bases; growing in moist to wet woods; somatic chromosome number 28.

Range: From southeastern Connecticut and New York south to central Florida and eastern Texas and west to extreme eastern Texas, eastern Tennessee, southwestern Pennsylvania and eastern New York. In 1931 Nieuwland and Just (Am. Midl. Nat. **12**: 217–220.) described the species *Arisaema deflexum*, from Tamarack Swamp, Turkey Creek Road, Indiana. They reported it to occur in the swamps of the northernmost counties of Indiana and across the boundary in Michigan. Although the author has not seen specimens, he considers it to be *A. triphyllum* subsp. *pusillum*. This would extend the range of the subspecies into the region around the foot of Lake Michigan where a number of coastal plain species have previously been found (see Peattie, D. C., 1922. Rhodora **24**: 57–70, 80–88.).

A. TRIPHYLLUM subsp. **Stewardsonii** Huttleston, comb. nov., based on *A. Stewardsonii* Britton, Man. Fl. N. U. S. ed. 2. 1057. 1905.

Plants with veins of scapes and leaf-sheaths usually prominent; leaflets narrow, light green, but not glaucous, beneath; lateral leaflets slightly oblique at bases and slightly to moderately gibbous on outer margins, acutely angled at bases; spathe-tubes green with very prominent white flutings or ridges, with narrow or moderately broad flanges, 1–3 mm., at tops; insides of laminae variously marked with purple or purple-brown, most frequently green with purple markings only in the throats, but often purple strongly striped with green, never wholly purple and rarely wholly green; growing in wet, boggy, shaded locations; somatic chromosome number 28.

Range: In northeastern North America from Prince Edward Island, southern Quebec and northwestern New York south and west to western Pennsylvania, northern New Jersey and in the mountains to western North Carolina. One specimen in the Academy of Natural Sciences of Philadelphia was collected by C. C. Deam eight miles east of Michigan City, Laporte County, Indiana, in May, 1932.

Wiegand and Eames in *The Flora of the Cayuga Lake Basin, N. Y.*, p. 134, 135 (1925) mentioned having found plants along the Clyde River southwest of Clyde that were intermediate between *A. triphyllum* subsp. *triphyllum* and subsp. *Stewardsonii*. This author has visited that area and found large numbers of plants growing in low, wet woods which resemble subsp. *Stewardsonii* in habit, leaf-shape, and spathe-tube fluting, but they displayed marked glaucescence on the dorsal surfaces of the leaves. Most of these plants had a character which is not common to either of these subspecies. The two sides of the spathe-tube did not overlap in front but barely met so that a slit was evident in the front of the tube from the top to the base. Despite the fact that subsp. *Stewardsonii* has been characterized by a spreading spathe-tube which forms a V-shaped slit in front, at no other place has the author seen spreading nearly so extreme as in this one loca-

tion. The author has made chromosome counts of six such plants. Two of these had 42 somatic chromosomes and the other four had 28. Specimen number 42 in the Wiegand Herbarium is one of the former plants and numbers 35, 37, and 38 are three of the latter. The author considers this group of plants to have arisen as hybrids between the two subspecies *triphyllum* and *Stewardsonii*. The fact that two of the plants appear to be triploids arising from plants with 28 and 56 somatic chromosomes upholds this opinion. Nothing is known of the fertility of these plants.

Discussion of the Relationships of Subspecies. A large number of characteristics have been suggested to separate the three subspecies. This writer has found that most of these criteria, when studied carefully throughout the range, break down and cannot be used as key characters. Below is a discussion of the value of the proposed differences.

Habitat. Subsp. *triphyllum* grows in moist, but not wet, locations along watercourses. The other two subspecies are found growing in wet, boggy locations. Occasionally the typical subspecies is found in swamps associated with one or both of the others. Similarly, subsp. *pusillum* and *Stewardsonii* are occasionally found in drier ground near subsp. *triphyllum*.

Habit. As a general rule, the typical subspecies is a stout plant whereas the other two are more slender. It is, however, difficult to measure the degree of stoutness and the overlap between the extremes is so great that the character cannot be used as a definite distinguishing point, but it merely contributes to the separations of the subspecies.

Time of flowering. Subsp. *triphyllum* is the first to flower in the spring. From one to two weeks after this, subsp. *Stewardsonii* begins flowering and subsp. *pusillum* begins approximately two or three weeks after subsp. *triphyllum* has begun. It is not unusual, however, to find all three in flower at the same time since each of them continues flowering for a number of weeks.

Leaf color. Subsp. *Stewardsonii* tends to have dark green leaves while the leaves of the other two subspecies are lighter. Only the typical variant shows glaucescence on the dorsal surfaces of the leaves and in these plants it is very marked when the leaves are mature. Although the leaves of the other two subspecies are somewhat lighter beneath, they are not glaucous. As has been pointed out under the discussion of subsp. *Stewardsonii*, in a location southwest of Clyde, New York, numerous specimens, which were otherwise this subspecies, do show glaucescence. It is very possible that other locations will be found where this is the case.

Leaf shape. The leaflets of subsp. *triphyllum* tend to be broadly ovate or obovate whereas those of both other subspecies tend to be narrowly ovate or lanceolate. There is considerable overlap in this respect. The lateral leaflets of the first variant are usually strongly gibbous on the outer margins and

obtusely angled at the bases. Those of the other two subspecies are never strongly gibbous or obtuse at the bases, but are moderately to slightly gibbous and narrowly to moderately acute. Considerable gradation is displayed here also.

Spathe-lamina color. The coloration of the insides of the spathe-laminae varies from unmarked purple through various degrees of striping with green or whitish to unmarked light green. Those of the typical subspecies cover the entire range of variation, but are very rarely wholly purple and are usually purple marked with prominent green or whitish stripes from the base to the tip. Those of subsp. *Stewardsonii* are never wholly purple and approximately 75 per cent are green, more or less marked with purple between the veins in the throats only. Occasionally plants of this group are found which have unmarked green spathe-laminae and they are commonly purple, prominently striped with green. Nearly all of those of subsp. *pusillum* are wholly purple with stripes evident only at the bases or unmarked green in about a 3:1 ratio respectively. Occasionally a plant is found with narrow, green stripes on the purple lamina. In these, most frequently, the one stripe follows the central vein. Inasmuch as all the color phases displayed by one subspecies can be found in one colony with one coloration grading imperceptibly into another, it seems impractical to affix names to them. This author feels that the use of the terms "the striped variety," "the purple variety," or "the green variety" will suffice.

Spathe-lamina shape. It has been suggested that the shape of the spathe-lamina can be used to separate the subspecies. Here again, there is a tendency toward a separation, but the degree of variability and the overlapping make the character of questionable value. That of subsp. *pusillum* tends to be narrowly ovate with a long acuminate tip. That of subsp. *triphyllum* tends to be ovate with a short acuminate or acute tip and that of subsp. *Stewardsonii* tends to be broadly ovate with a short acute tip.

Spathe-tube flange. The breadth of the flange or deflexed portion at the top of the spathe-tube is fairly good as a separation character. Subsp. *triphyllum* has a broad flange, 2–7 mm. Subsp. *Stewardsonii* has a moderate flange, 1–3 mm., and subsp. *pusillum* has a very narrow flange, 1–2 mm. Actual measurements cannot be used since the flange of a small plant of the first might be narrower than that on a large plant of the last.

Spathe-tube. The fluting of the spathe-tube is the best character for separating subsp. *Stewardsonii* from the other two. The tube in that subspecies is always very strongly ridged or fluted whereas in the other two it is obscurely fluted, if at all. Wiegand and Eames (Fl. Cayuga Lake Basin 134 & 135. 1925.) characterized subsp. *Stewardsonii* as having a V-shaped opening between the margins of the tube at the top. This character does not hold throughout the range of the subspecies.

Spadix shape. The spadix of *A. triphyllum* subsp. *triphyllum* is more or less clavate whereas the spadices of subsp. *pusillum* and *Stewardsonii* are cylindric or subcylindric. The difference, however, is too fine to be of much value.

Seed shape. Prof. M. L. Fernald (Rhodora **42**: 247–253 *ill.* 1940.) proposed a seed character as a separation point. He stated that seeds of subsp. *pusillum* and *Stewardsonii* were invaginated at the base around the hilum, whereas those of subsp. *triphyllum* were not. This author has not been able to demonstrate any correlation in this characteristic.

Chromosome number. This author has made about fifteen chromosome counts of subsp. *Stewardsonii* and seven of subsp. *pusillum* and found them to be 2n = 28. Of about 50 counts made by the author on subsp. *triphyllum*, all except two were 2n = 56. The two exceptions were 2n = 28 and both specimens were collected by the writer in Big Gully, Cayuga County, New York. Atkinson (Bot. Gaz. **28**: 1. 1899.) reported the gametic number of *A. triphyllum* as 16 and Bowden (Am. Jour. Bot. **27**: 357–371. 1940.) reported the species to have 56 somatic chromosomes. Since no specimens are available, it is impossible to ascertain from what subspecies these counts were made.

In this author's opinion, a mere difference in chromosome number, particularly the difference between diploid and tetraploid, is not adequate reason for the erection of separate species. In addition there must be sufficient morphological difference between two populations of plants to render any given plant assignable to one or the other species. Even though several characteristics contribute to the separation of these three populations, most of these characters are quantitative and it is frequently difficult or impossible, particularly with pressed specimens, to assign individual plants to one population. True, a tetraploid should not be expected to hybridize freely with a diploid, but this author has found two specimens of the tetraploid subspecies *triphyllum* at Big Gully, Cayuga County, New York which had 2n = 28 chromosomes. It is very possible that these diploids are considerably more common than these findings would indicate. In the case of subsp. *pusillum* and *Stewardsonii* only quantitative characters serve to separate the two. Even though the two populations are partially separated geographically, this writer has found one swamp at Clintondale Station, Ulster County, New York where both subspecies grow together with a number of intermediates. It is felt that the separations between these three populations are something less than those required between species, and thus the populations have been described as subspecies.

It is very probable that the three subspecies arose from one original population in North America. The question of how they arose, on the other

hand, is not as easy to answer. Two interpretations appear to be indicated. In the first place, the original population could have split into two, subsp. *Stewardsonii* which was hardier and spread north and subsp. *pusillum* which spread south. At one time a hybrid arose between these two and its chromosome number was or became doubled resulting in an allotetraploid. If this is the explanation, it is to be expected that the tetraploid would combine the characters of the two diploids. When one analyzes the characteristics of the three subspecies, it is immediately evident that this is not the case. The tetraploid, *A. triphyllum* subsp. *triphyllum*, in the characters of habitat, habit, time of flowering, leaf shape and width of spathe-tube flange falls, not between the other two subspecies, but to one side of both of them. It is true that these characters might be thrown out as being due to the increased vigor of the tetraploid, but it would be difficult to explain away the glaucescence of the leaf and the clavate shape of the spadix on this basis. The other interpretation which seems to be indicated, and the one which is favored by this author, is that the original population gave rise to three separate populations and that the chromosomes in one of them were or became doubled. This tetraploid, then, being more vigorous, spread more rapidly and widely than the diploids. This interpretation would allow for the presence of the characteristics of the tetraploid which differ from those of either of the other subspecies. The presence of diploids which apparently cannot be separated from the tetraploids would be further proof of this interpretation.

SUMMARY

A study has been made of the eastern American jack-in-the-pulpits that have, in the broad sense, been considered as *Arisaema triphyllum*. These comprise a single species consisting of three major races. One of these races is widespread in eastern North America and, seemingly, predominantly tetraploid. The two others are diploid and more restricted in range. Of these, one is essentially northern and upland; the other is essentially southern and coastal. A sufficient degree of overlapping in the morphological characters has been found to support the treatment of these three races as subspecies, rather than full species. Restudy of the elements concerned in the original publication of *Arum triphyllum* L., the basonym of *Arisaema triphyllum*, indicates that the widespread tetraploid should be considered as the typical element and it is here designated as subsp. *triphyllum*. The other two subspecies are designated as subsp. *Stewardsonii* and *pusillum*. It is considered most probable that these three races arose from a common stock, with subsequent geographical and ploidal divergence of morphological types.

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CYTOLOGICAL EVIDENCES OF HYBRIDIZATION BETWEEN JUNIPERUS VIRGINIANA AND J. HORIZONTALIS

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Colonies of presumed interspecific hybrids within the genus *Juniperus* have been observed by Fassett (1944 b, 1945 a, 1945 b,) in certain areas where the geographic ranges and ecological habitats of two species overlap. On the eastern edge of the Driftless Area of Wisconsin, and along the coast of Maine, colonies composed of individuals with characteristics intermediate between those of *Juniperus virginiana* L. and *J. horizontalis* Moench have been observed. In general the range of *J. virginiana* lies southward and that of *J. Horizontalis* to the north of these regions (Fassett 1945 b). Except in the areas of overlap, each of the species has a characteristic combination of characters. More information on the nature of individuals in colonies situated in such regions has now been sought through a cytological investigation.

Materials and Methods The colonies selected for studies of the presumed hybrids were those occurring within the eastern fringes of the Driftless Area in southwestern Wisconsin. Identifications of presumed hybrids were made by the method described by Fassett (1945 b). The locations of these colonies, as well as those of the putative parental species which were investigated, are indicated on a map of northeastern U.S.A. (fig. 1).

Preparations suitable for the study of somatic metaphase chromosomes were obtained from tissue of immature leaves or cones treated for 3–4 hours in a saturated aqueous solution of paradichlorobenzene before fixation in acetic alcohol (1 : 3) for one half hour longer. After hydrolysis in 1N HCl for 8 minutes at 60° C, the material was stained in aceto-carmine.

Meiosis was studied in pollen mother-cells from male cones collected during July and August, 1946. Good fixation of this material was not the rule. Of the killing agents used (Carnoy's, Fleming's, and Craf) a modification of Carnoy's fixative (6 abs. alcohol : 2 glacial acetic acid : 1 chloroform) was found superior though not dependable. The aceto-carmine squash technique gave the most satisfactory preparations. Meiosis in *J. horizontalis* was found to occur from the middle to the end of July and in *J. virginiana* from the

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middle to the end of August, while in most of the individuals in the hybrid colonies it occurred in the intervening time. A comparative measure of irregularity at meiosis for each individual was obtained by inspecting 100 pol-

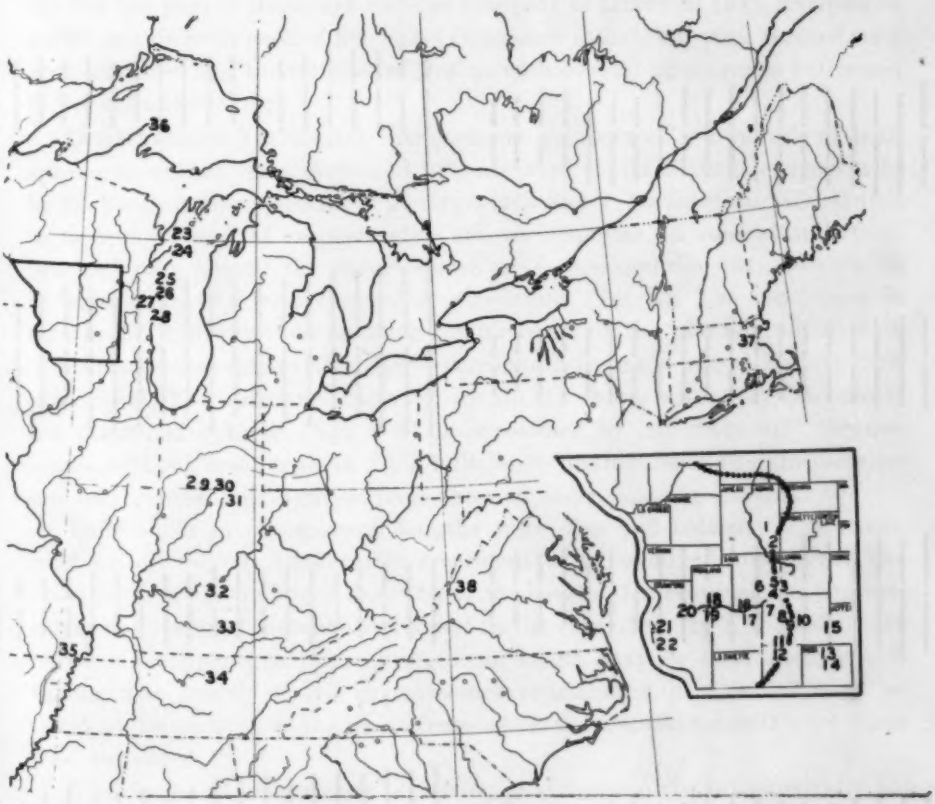
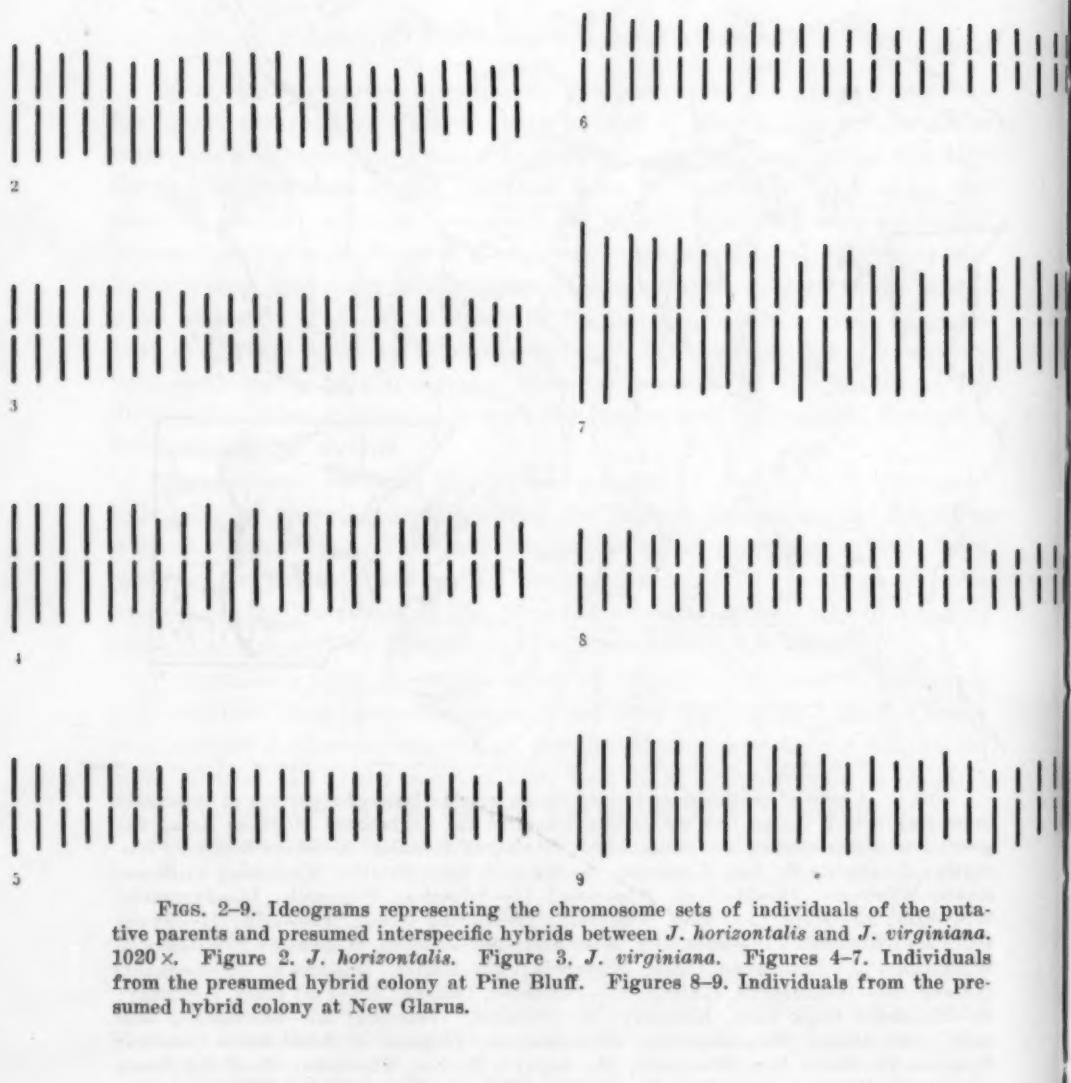


FIG. 1. A map of northeastern United States with an inset of a portion of Wisconsin indicating with a dotted line the eastern limits of the unglaciated Driftless Area. The general locations studied are indicated. *J. virginiana* Colonies: Numbers 3—Okee, Wisconsin; 5—Prairie du Sac, Wisconsin; 6—West of Sauk Prairie, Wisconsin; 7—Mazomanie, Wisconsin; 10—Madison, Wisconsin; 13—Edgerton, Wisconsin; 14—Janesville, Wisconsin; 15—Hope Lake Bog, Wisconsin; 16—Spring Green, Wisconsin; 17—Tower Hill Park, Wisconsin; 18—Sauk City, Wisconsin; 19—Muscoda, Wisconsin; 20—Boscobel, Wisconsin; 21—Prairie du Chien, Wisconsin; 22—Bagley, Wisconsin; 29—Lebanon, Indiana; 30—Indianapolis, Indiana; 31—Pendleton, Indiana; 32—Fort Knox, Kentucky; 33—Mammoth Onyx Cave, Kentucky; 34—Gallatin, Tennessee; 35—Bloomsdale, Missouri; 37—Boston, Massachusetts; 38—Lexington, Virginia. *J. horizontalis* Colonies; Numbers 23—Sister Bay, Wisconsin; 24—Bailey's Harbor, Wisconsin; 25—Point Beach State Park, Wisconsin; 26—Two Rivers, Wisconsin; 27—Elkhart Lake, Wisconsin; 36—West Bluff, Keweenaw Point, Michigan. Presumed hybrid Colonies: Numbers 1—Sec. 33-T.17N-R.6E, Wisconsin; 2—Grand Marsh, Wisconsin; 4—Black Hawk Lookout, Wisconsin; 8—Black Earth, Wisconsin; Cross Plains, Wisconsin; 9—Pine Bluff, Wisconsin; 11—Belleville, Wisconsin; 12—New Glarus, Wisconsin.



FIGS. 2–9. Ideograms representing the chromosome sets of individuals of the putative parents and presumed interspecific hybrids between *J. horizontalis* and *J. virginiana*. 1020×. Figure 2. *J. horizontalis*. Figure 3. *J. virginiana*. Figures 4–7. Individuals from the presumed hybrid colony at Pine Bluff. Figures 8–9. Individuals from the presumed hybrid colony at New Glarus.

len mother-cells at the two-nucleate or four-nucleate stage; or, if a study of meiosis could not be made, 400 immature pollen grains were examined.

Collections of male cones containing almost mature pollen were made during the last part of February and the first part of March in 1947. Samples of pollen grains from each of five cones from each individual were stained with aceto-carmine and the number of grains with normal appearance expressed in per cent of the total.

Observations The somatic chromosome numbers of individuals of both species as well as their presumed hybrids were found without exception to be 22. Somatic chromosomes of *J. virginiana* and *J. horizontalis* (illustrated in figures 10 and 11 respectively) are very similar. A somewhat heterobrachial pair among the chromosomes of *J. horizontalis* distinguishes its ideogram (fig. 2) from that of *J. virginiana* (fig. 3). The ideograms in figures 2–9 represent chromosome complements of the plants studied, with the chromosomes arranged in decreasing length from the left with short arms uppermost. The unbalance observed within the chromosome complements of the presumed hybrids (figs. 4–9) is occasioned by heterobrachial chromosomes without counterparts. This unbalance distinguishes the chromosome sets of the presumed hybrids from those of their putative parents.

Differences in chromosome lengths were observed between cells examined within the one tissue after treatment with paradichlorobenzene. The shortening is presumably a function of the length of time which the chromosomes have been at metaphase. Except in the case of figure 7, the difference between ideograms in total chromosome length may be attributed to this factor. The length of the chromosomes represented in figure 7 may be taken as the norm since the tissue from which these measurements were made was untreated.

The degree of irregularity occurring at meiosis in the taxonomically acceptable members of both putative parents was first investigated. Pairing proceeded normally during prophase and subsequent irregularities were few. The total number of chiasmata observed at metaphase of both species varied from 21 to 24 per pollen mother-cell. With the exception of a bridge-fragment configuration (fig. 21) observed in an individual of *J. horizontalis*, the only type of irregularity noted was the presence of micronuclei or their precursors, lagging chromosomes. In table I the average percentages of irregularities at meiosis are indicated for a number of plants of both the species and presumed hybrids.

Members of the New Glarus and Pine Bluff colonies, both located on sandstone hillsides, were selected for detailed study of the presumed hybrids. At New Glarus all plants were creeping with the exception of one upright individual. Other specific characters, however, occurred in apparently ran-

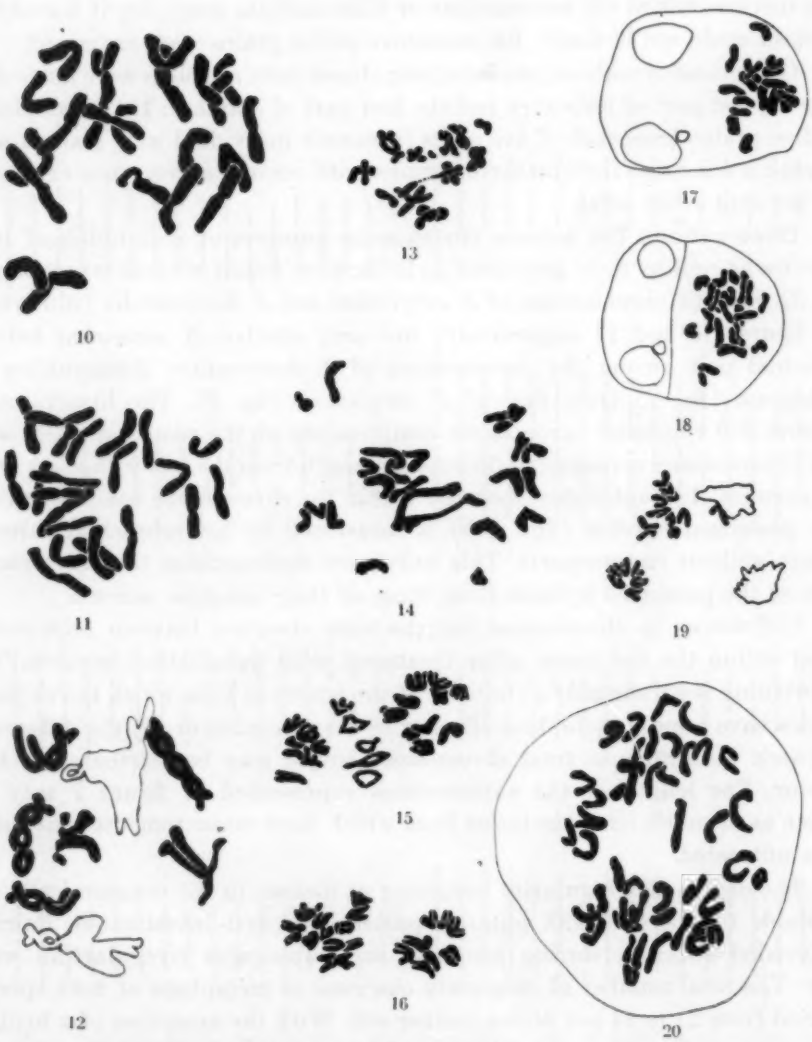


FIG. 10. Somatic chromosomes of *J. horizontalis* from Colony number 27, 970×. FIG. 11. Somatic chromosomes of *J. virginiana* from Colony number 10, 970×. FIG. 12. Diakinesis in a presumed hybrid from the Pine Bluff colony showing two associations which could not be interpreted, 970×. FIG. 13. Anaphase I in a presumed hybrid from the New Glarus colony showing a bridge and fragment as well as two unpaired chromosomes, 610×. FIG. 14. Anaphase I in a presumed hybrid (New Glarus plant number 6), indicating the occurrence of unpaired chromosomes and also two bridge-fragment configurations, 970×. FIG. 15. Anaphase I in a presumed hybrid (New Glarus plant number 6), showing univalents dividing at the equator, 610×. FIG. 16. Anaphase I in a presumed hybrid (New Glarus plant number 6), showing 8 chromosomes at one pole and 14 at the other, 610×. FIG. 17. Second meiotic division in a presumed hybrid (New Glarus plant

dom combinations. The colony at Pine Bluff contained individuals with all specific characters occurring in apparently random combinations. More meiotic irregularities were found in members of the New Glarus colony than in those at Pine Bluff. In a semi-erect plant at Pine Bluff (plant number 23) nearly all sporangia were aborted, while the remainder contained clumped pollen mother-cells abnormal in appearance. It is not included in table I.

TABLE 1. *Average percentage of cytological irregularities observed at microsporogenesis in the species and their presumed hybrids.*

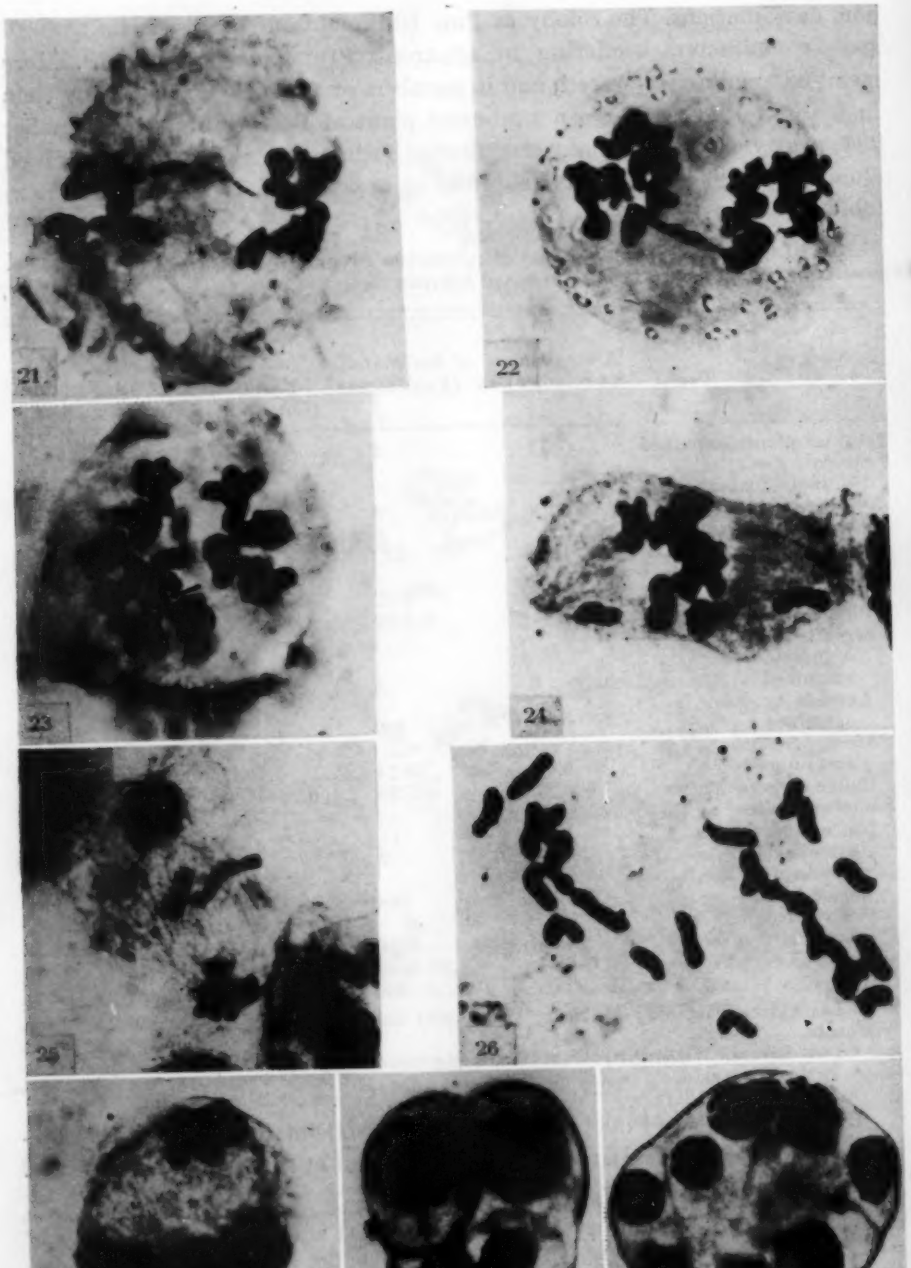
	J. virginiana (4 colonies)[1]	*J. horizontalis* (3 colonies)[2]	Presumed hybrids	
			New Glarus (Colony no. 12)	Pine Bluff (Colony no. 9)
Total no. plants examined	11	8	6	10
2-nucleate p.m.c.'s:				
No. individuals examined	8	8	5	9
Average no. p.m.c.'s examined	252	313	243	268
Mean percentage irregularity	0.19	0.32	5.56	1.54
Range of percentages	0–0.91	0–1.90	1.00–20.00	0–12.50
4-nucleate p.m.c.'s:				
No. individuals examined	9	8	6	10
Average no. p.m.c.'s examined	281	460	335	350
Mean percentage irregularity	0.02	0.24	20.10	1.00
Range of percentages	0–0.22	0–1.18	0.98–56.62	0–6.50
Immature pollen:				
No. of individuals examined	10	3	2	1
Average no. p.m.c.'s examined	1509	598	1024	440
Mean percentage irregularity	0.05	0.24	7.55	0
Range of percentages	0–0.41	0.20–0.32	6.96–8.14	0

[1] Lexington, Virginia; Madison, Wisconsin; Bagley, Wisconsin; Prairie du Chien, Wisconsin.

[2] Two Rivers, Wisconsin; West Bluff, Keweenaw Point, Michigan; Terry Andrae State Park, Wisconsin.

In members of the Pine Bluff colony, bridge-fragment configurations, lagging chromosomes and micronuclei were observed at the two-nucleate stages.

number 6) showing lack of coincidence of the two divisions, 610×. FIG. 18. Second meiotic division in a presumed hybrid (New Glarus plant number 13) showing a lack of coincidence of divisions and also a cell wall between the two sides, 610×. FIG. 19. Anaphase II in a presumed hybrid (New Glarus plant number 6) showing 7 chromosomes at the one pole and 10 chromosomes at the other, 610×. FIG. 20. Anaphase II in a presumed hybrid (New Glarus plant number 6) showing non-orientation of the chromosomes, 970×.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The percentage of these irregularities varied between individuals. At diakinesis a semi-prostrate plant at Pine Bluff (plant number 26) had in most cases 4–6 bivalents, and generally two other associations containing the rest of the chromosomes (fig. 12). These multiple associations usually resolve into pairs at metaphase though occasionally there is an apparent connection between different bivalents (fig. 23). The number of contact points that may be counted as chiasmata in the metaphase chromosomes of this plant varied from 18 to 23 per pollen mother-cell. In some cases, both in this plant and in others, two unassociated chromosomes were observed at metaphase I (fig. 24). Structural heterozygosity was also indicated by the observation of bridges at first anaphase (fig. 22).

Associations of groups of bivalents at prophase were seen less frequently in pollen mother-cells of individuals from the New Glarus colony, but, again, structural heterozygosity was indicated by the occurrence of bridge-

TABLE 2. *Distribution of chromosomes at first anaphase in pollen mother-cells of New Glarus plant no. 6.*

Distribution Categories					
0–22	1–21	2–20	3–19	4–18	5–17
0	0	0	2	1	3
Distribution Categories					
6–16	7–15	8–14	9–13	10–12	11–11
1	2	6	2	2	2

fragment configurations (figs. 13 and 14) and the presence of laggards at anaphase I and II. In some cells of a creeping individual at New Glarus (plant number 6) laggards were observed to be dividing at anaphase I (fig. 15), while in others, their division presumably took place at anaphase

FIGS. 21–29. Photomicrographs of meiosis in one putative parent and in presumed hybrids of *Juniperus horizontalis* and *J. virginiana*, 1020×. FIG. 21. Anaphase I in *J. horizontalis* showing a bridge and fragment. FIG. 22. Anaphase I in a presumed hybrid (Pine Bluff plant number 26) showing a bridge. FIG. 23. Metaphase I in a presumed hybrid (Pine Bluff plant number 26) showing 11 bivalents with an arrow pointing to what appears to be an association between two bivalents. FIG. 24. Metaphase I in a presumed hybrid (Pine Bluff plant number 26) showing two unpaired chromosomes. FIG 25. Telophase I in a presumed hybrid (New Glarus plant number 6) showing three lagging chromosomes which do not appear double and therefore may divide during the second division. FIG. 26. Metaphase I in a presumed hybrid (New Glarus plant number 6) showing almost complete lack of association of the chromosomes. FIG. 27. Interkinesis in a presumed hybrid (New Glarus plant number 6) illustrating a gross difference in size of the polar groups. FIG. 28. "Tetrad" stages in a presumed hybrid (New Glarus plant number 6) showing different nuclear sizes. FIG. 29. "Tetrad" stages in a presumed hybrid (New Glarus plant number 6) showing different nuclear sizes. FIG. 29. "Tetrad" stages in a presumed hybrid (New Glarus plant number 6) showing supernumerary nuclei.

II (fig. 25). In many cells most of the chromosomes were unassociated at metaphase I (fig. 26) and the total number of chiasmata was in many cases as low as 7 or 8. Examination of pachytene, however, indicated no unpaired strands. Unequal distribution was often noted at anaphase I. In figure 16 there are 14 chromosomes at one pole and 8 at the other. Only two anaphase I figures out of the 21 examined on this same slide had 11 chromosomes at each pole. All distributions other than 0:22, 1:21, 2:20 were found (table II). The pronounced difference often noted in size of the two groups is illustrafed in figure 27.

TABLE 3. *Percentages of apparently normal pollen of the species and their presumed hybrids.*

Classification	Total no. of Plants	Mean no. Examined per Plant	Mean per Cent with Normal Appearance	Range of Percentages
J. virginiana (21 colonies)	80	602	98.1	88.5–100
J. horizontalis (7 colonies)	24	579	99.2	95.0–100
Colonies of Presumed Hybrids				
New Glarus (Colony No. 12)	10	551	79.9	59.5–94.5
Pine Buff (Colony No. 9)	20	870	87.1	46.0–99.5
Belleville (Colony No. 11)	8	537	94.9	75.0–100
Black Earth (colony No. 8)	8	827	97.4	91.5–100
Grand Marsh (Colony No. 2)	6	500	98.5	97.5–99.5
S 33–T17N–R6E (Colony No. 1)	3	500	98.5	97.0–99.0
Cross Plains (Colony No. 8)	7	1004	98.6	97.0–99.5
Blk. Hawk Lkt. (Col-No. 4)	3	500	99.3	99.0–99.5

At the four-nucleate stage most of the irregularities in members of both the Pine Bluff and New Glarus colonies consisted mainly of laggards or micronuclei. Unequal distribution noted in certain members of the New Glarus colony at anaphase II, (fig. 19), may result in two large and two small nuclei similar to those shown in figure 28. In some cases (fig. 20), almost complete disorientation of the chromosomes was found at division II. These clumps of chromosomes would presumably later form many nuclei of varying sizes as shown in figure 29. Lack of coincidence of the second nuclear divisions was often observed in some individuals of the New Glarus colony (figs. 17 and 18). A cell wall was sometimes found between the nuclei in the binucleate stage (fig. 18) while at other times it is lacking until after

the four-nucleate stage is reached, at which time the cross walls are formed concurrently.

Examinations of immature pollen of two individuals in the New Glarus colony disclosed a great number of pollen grains with micronuclei. Some pollen grains contained two nuclei, others were aborted or minute. Immature pollen was examined from only one individual at Pine Bluff; no irregularities were observed.

The percentages of apparently normal pollen, indicated in table III, were found to be high in individuals of both species. Certain individuals of *J. virginiana* had lower percentages of apparently normal pollen than any plant of *J. horizontalis* but the mean percentages, 98.1 for the former and 99.2 for the latter, differed by only 1.1%.

The pollen of certain individuals which on morphological grounds were presumed to be of hybrid origin, contained considerably more defective grains than were observed in any individual of the putative parent species. For example, two individuals in the New Glarus colony were observed to have only 59.5% apparently normal pollen. Though the mean percentage is higher for individuals in the Pine Bluff colony, the range extends lower than for individuals in the New Glarus colony. Individuals in other presumed hybrid colonies showed little evidence of defective pollen. The most heterogeneous colonies, namely New Glarus and Pine Bluff, Fassett (1945 a), were found to have considerably lower averages of good pollen than either of the species or any of the more homogeneous presumed hybrid colonies.

Discussion On taxonomic evidence presented by Fassett (1945 b), and substantiated by this study, heterogeneous colonies occurring in the Driftless Area of Wisconsin may be presumed to be either the variable progenitors from which these two species have stemmed or they may be hybrids originating from the meeting of the two species owing to an overlap of their ecological habitats. A measure of credibility could be given the former since it is believed that certain elements of the flora in the Driftless Area survived the various glacial periods, but Fassett (1945 b) has described similar colonies on the coast of Maine where the ranges of the two species overlap in an area known to be entirely glaciated. The hypothesis that these colonies are of hybrid origin therefore appears to be the more probable. The cytological data collected in this study favor further the assumption of hybridity.

The one pair of chromosomes that is distinctly heterobrachial in the complement of *J. horizontalis* should be recognizable among the chomosomes of an F_1 hybrid of this species with *J. virginiana*, which has no heterobrachial chromosomes. Since these chormosomes could not be identified with assurance in the sets of the presumed hybrids examined, it is possible

that these plants may be backcross progeny to *J. virginiana* or of later hybrid generations. The presence of other heterobrachial chromosomes without counterparts was noted in the ideograms of the presumed hybrids. These may have originated through crossing over within homologous areas situated in different parts of the members of a bivalent, or through aberrancies such as have been observed in the presumed hybrid material caused by crossing over within inversions or translocations. Emsweller and Jones (1938) have reported the occurrence of different morphological types of post-meiotic chromosomes in the interspecific hybrid *Allium cepa* × *A. fistulosum*. They consider these "new" chromosomes to be formed by crossing over between the two genomes as postulated here.

The unpaired chromosomes seen in varying numbers at different metaphases of pollen mother-cells of some individuals at New Glarus may indicate that the homology of their chromosomes is less than that observed in the species. The almost normal pairing observed at pachytene indicates that the unpaired chromosomes at metaphase are desynaptic rather than asynaptic. Pairing of nonhomologous chromosomes has been observed by McClintock (1933) in maize, and also by Levan (1942, 1945) in haploid rye and haploid sugar beets. The possibility of all so-called "asynaptic" chromosomes being actually the result of desynapsis is suggested by Li, Pao and Li (1945) but Huskins and Wilson (1938) show that in *Trillium* two types of asynapsis as well as desynapsis can be differentiated when the coiled chromonemata with their changes of direction can be analyzed. This is not possible in *Juniperus*. Andersson (1947) states that the "asynaptic" chromosomes which he found in *Picea abies* were observed to be paired at pachytene and to separate gradually as the prophase progresses. The types of aberrancies reported by him are somewhat similar to those reported in this study though he found unpaired chromosomes in greater numbers. Evidence of structural hybridity was not observed and the "asyndetic" condition was attributed to genetic causes. The taxonomic characters of the asynaptic spruce were typical of the species as were also those in the same colony. Whether the occurrence of unpaired chromosomes at first metaphase of meiosis in New Glarus plant number 6 is gene-determined or due to the lack of homology of the chromosomes cannot be ascertained from the facts at hand. If the latter, the hybrid nature of these plants is strongly indicated.

The difference in timing occasionally noted in the division process of different nuclei within pollen mother-cells of New Glarus individuals was also noted to a slight degree in an individual of *J. horizontalis*. Either a mechanical or genic change in the chromosomal constitution may be responsible for disturbing the equilibrium of the meiotic process.

The effect of environment on the meiotic process cannot be discounted

when sterility phenomena are being considered. Pine Bluff plant number 23, which contained aborted sporangia in the male cones, was somewhat shaded by an oak tree growing nearby. As early as 1908 Tischler found that lack of light caused the formation of a high proportion of bad pollen in two species of *Potentilla* and in their hybrid it caused complete sterility. He maintained that the effect of lack of light in causing pollen sterility was disproportionately greater on the interspecific hybrids than on the species. As shown in extensive studies by Oehlkers (1937) the general physiological state of the plant is reflected in the number of chiasmata formed at prophase. The abortion noted in Pine Bluff plant number 23 may have been at least partly a result of shading. Shading could not have been responsible for the sterility noted in the New Glarus colony, since these plants were in a favorable position on an open hillside. The low number of chiasmata and the many unpaired chromosomes observed in pollen mother-cells of New Glarus number 6 probably may be attributed to causes other than environment.

Differences in levels of pollen fertility and in degrees of irregularity at meiosis between presumed hybrid colonies may be an indication of the age of the colony. Irregularities at meiosis would tend to be eliminated during sexual reproductions since only gametes with a balanced genic constitution would be viable. Therefore, such colonies as those at Black Earth and Cross Plains which appear to have little or no pollen sterility, may have originated many generations ago, and have spread from the point of hybridization throughout the surrounding area. In some isolated colonies all individuals have certain characters of one or the other of the species, while the other characters occur at random. The large amount of pollen sterility and the high percentage of meiotic irregularities noted in New Glarus individuals may indicate that this colony is the progeny of recent hybridizations. Two trees with the characteristics of *J. virginiana* were noted in that vicinity as were also individuals with the taxonomic features of *J. horizontalis*. The absence of individuals with intermediate growth habits cannot be explained on the premise of recent hybridization, unless it is supposed that the creeping habit is dominant and the individuals are all F_1. It is possible, though unlikely, that some selective force may favor the creeping individuals and prevent the appearance of the semi-prostrate habit. This colony could also conceivably be the progeny of a back-cross of an F_2 or F_3 individual to *J. horizontalis*, but the low fertility observed makes this hypothesis improbable.

The small number of individuals intermediate between the two species growing side by side on the hilltop and hillside at Grand Marsh, may be explained by postulating as does Fassett (1945 b) that at this point some internal barrier exists between the species. The normal appearance of the pol-

len of these intermediate types may indicate that they are the successful progeny of an ancient hybridization, but the possibility that they may be F_1 progeny cannot be discounted since normal pollen has been reported in the F_1 of species crosses (Huskins 1929). Different strains of the same species may give species hybrids of quite different behavior as previously discussed. Likewise, the internal barrier to hybridization which may exist between the individuals of the species at Grand Marsh may not be present in other strains of these species. A somewhat similar situation may exist at Elkhart Lake, Wisconsin, (colony number 27) which conformed taxonomically to *J. horizontalis*. The presence of berries with seeds was noted on the female individuals, which as far as could be determined could have received pollen only from *J. virginiana*. Though seeds were found to be set, no intermediate individuals occurred in the vicinity.

Since the colony at Pine Bluff was initially selected as the critical material for this study, corresponding pollen and meiotic studies were made on the same trees. The percentage of apparently normal pollen was not always what might be expected through an examination of the meiotic process. In some plants meiosis was regular and pollen appeared normal, in other trees meiosis was regular and yet considerable pollen was aborted, and in another case meiosis was somewhat irregular but the pollen appeared normal. Variability in the amount of apparently normal pollen among cones was found and it may be possible that, since in certain cases the pollen sample was taken from a different part of the tree than was the sample for meiosis, the discrepancy may be due to environmental effects. In cases where no irregularities were observed at meiosis and yet there was a great deal of pollen abortion, minute structural losses within the chromosomes may be responsible. The occurrence of a high percentage of good pollen after the observation of irregularities at meiosis cannot so readily be explained unless environmental effects may be operative in producing the latter. It is possible also that, though appearing normal, the pollen would carry deficiencies or duplications which would cause it to be nonfunctional. Peto (1938) also found in poplar hybrids apparently normal pollen from an individual whose meiosis was quite irregular. Closer examination disclosed minute debris which he interpreted as being aborted pollen grains. In the pollen from the plant under discussion here, however, such debris was not evident. In Pine Bluff plant number 23, there seems to have been abortion of pollen mother-cells before meiosis. The percentage of apparently normal pollen was considerably higher than might have been expected from the clumped pollen mother-cells observed in young sporangia. It is quite possible that some of the less sterile cones owe their greater fertility to a more fortunate situation with regards to light, translocation of food, temperature at a critical period, or to any of a variety of physiological factors.

As stressed by Huskins (1929) each one of the points concerning evidence for hybridity could be refuted if offered alone as a criterion. The appearance of chromosomes morphologically dissimilar to those of both species could be explained by supposing losses, inversions, and translocations of chromosome parts which may occur within one species. In fact, evidence of an inversion was found within *J. horizontalis* but neither was the meiotic process greatly disturbed nor did the pollen fertility appear reduced. "Asynapsis" controlled by a genetic factor has been observed in a number of species as has also pollen sterility. In addition, certain environmental influences may cause aberrancies resembling these irregularities. Even the sum of these cytological observations by themselves cannot be accepted as proof of hybridity but in conjunction with the taxonomic data the validity of this assumption is strengthened.

The length of time that would be involved in making a cross between these species and in studying their progeny, as recommended by Baker (1947), makes the experimental approach impracticable. Strains within the species may differ in their ability to cross. Such incompatible strains may be present at Elkhart Lake and at Grand Marsh. This points out a weakness in the experimental approach since failure to make a cross artificially may not mean that its occurrence is impossible in nature.

The extent of gene flow from these centers of hybridization does not seem to be great. At Pine Bluff the hybrid colonies are limited to the neighboring hillsides. An occasional presumably hybrid colony exists along the side of the valley between Cross Plains and Black Earth. There, the flow of genes of *J. horizontalis* into *J. virginiana* seems to have ended. Southward from Pine Bluff evidences of hybridization are found at Belleville and at New Glarus.

The competition afforded these hybrid forms by the species may account for their limitation to different area. The species are particularly adapted to the ecological habitats in which they are found and so would tend to prevent the spread of hybrid forms which probably would be less well adapted. These hybrid colonies, however, can be regarded as a reservoir from which gene flow may be expected if change of environment were to occur.

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SUMMARY

Colonies of presumed hybrids of *Juniperus virginiana* L. with *J. horizontalis* Moench have been observed on the eastern fringe of the Driftless

Area in Wisconsin where the geographic ranges and ecological habitats of these species overlap. Characters occuring in a characteristically different combination in each of the species are found in random combinations in these colonies.

A comparative study of the somatic chromosome complements of the species and several of the presumed hybrids revealed an unbalance in those of the latter, evidenced by the presence of heterobrachial chomosomes without counterparts. The highest percentage of irregularities found at meiosis in pollen mother-cells of any plant of *J. virginiana* was 0.91% of *J. horizontalis* 1.91% and of their presumed hybrids 56.62%. Besides being more numerous than those of the putative parents ,the irregularities of the presumed hybrids were of more diverse types, such as bridges, bridge-fragment configurations, laggards, micronuclei and different sized nuclei. The percentage of apparently normal pollen was found to range from 88.5 to 100% in *J. virginiana*, from 95.0 to 100% in *J. horizontalis*, and from 46.0 to 100% in the presumed hybrids.

This cytological evidence considerably strengthens the case for the occurrence of natural hybridization between *J. virginiana* and *J. horizontalis* first proposed by Fassett on standard taxonomic grounds.

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ON THE EMBRYOLOGY OF SWERTIA CAROLINENSIS

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The gentian family is widely distributed throughout both the old and new worlds and, as pointed out by Rendle (1925), its representatives include dry sand-loving species, marsh or floating water-plants, grass-land plants, and many alpine forms. In external characteristics, however, marked differences exist between the terrestrial and marsh forms and many authors now place the latter in a new family, the Menyanthaceae.

Stolt (1921), in reviewing the literature and in his studies of *Erythraea, Gentiana, Exacum, Chlora, Halenia, Menyanthes, Villarsia* and *Limnanthemum*, has shown that the two families differ as much cytologically as they do externally. In the Menyanthaceae, he observed that the embryo sac was rather small and elongated, an integumental tapetum was present, the antipodals were regularly three in number and degenerated early, and a cellular endosperm was formed. The Gentianaceae, on the other hand, was characterized by a rounded or oblong embryo sac, the absence of an integumental tapetum, three or more variously developed antipodals, and a free nuclear endosperm.

These observations did not embrace the genus *Swertia*, however, which forms a conspicuous part of our flora, and since very little work on the Gentianaceae has been done in this country, *Swertia carolinensis* (Walt.) Baill, was selected and studied in the light of the above findings. An abundance of material has made possible a study which has not only confirmed Stolt's observations, in part, but has also revealed certain facts not previously reported.

Swertia carolinensis exhibits several peculiarities, such as the presence of squamulae intravaginales, a growth period of six or seven years before blooming, a flowering shaft of seven or eight feet, and a distinctly succulent nature. The plant occurs commonly throughout the eastern portion of the United States where it is remarkably local in its distribution. Its tall and beautiful dichasial cymes of sympetalous flowers are quite attractive and, except for the two-carpellate gynoecium, are four-merous.

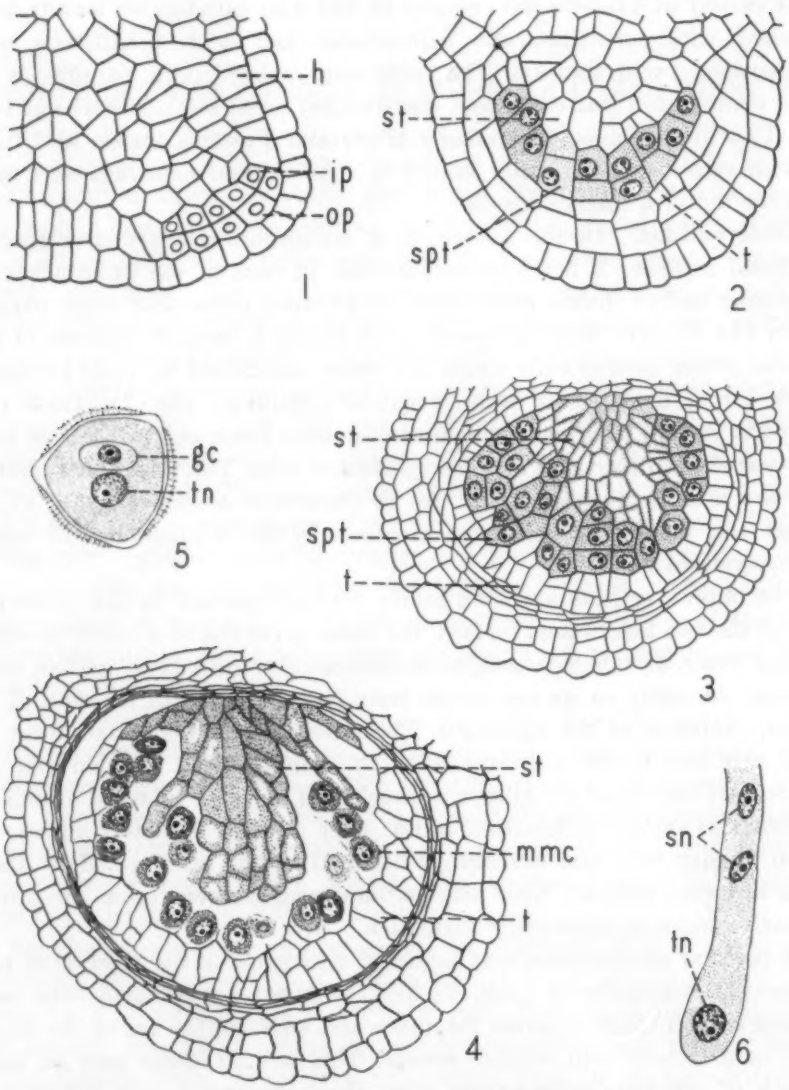
Material and Methods. Entire flower clusters, each containing several buds in different stages of development, were collected from early May to the end of the growing season. After removing the outer bracts, these clusters were split longitudinally and placed in the killing solution in the field. Upon returning to the laboratory the air was removed immediately by means of a suction pump.

A variety of fixatives were employed, the most satisfactory results being obtained with formalin-acetic acid-alcohol and with Schaffner's weak chromo-acetic acid solution. The buds were imbedded in paraffin in the usual manner and transverse and longitudinal serial sections were cut from 8 to 15 μ in thickness. Flemming's triple and Foster's tannic acid-ferric chloride stains were generally employed. All cellular drawings were made with the aid of a camera lucida.

Observations. In the anther, four microsporangia are developed in the usual manner. A few hypodermal cells in each of the prominences of the young anther divide periclinally to produce inner and outer parietal layers (fig. 1). The inner partietals give rise to a variable number of primordial pollen mother cells which are easily recognized by their polygonal shape, larger nuclei, and dense, granular cytoplasm (fig. 2). These cells extend in several irregular vertical rows in each theca and increase in number somewhat to form the microspore mother cells. The thin-walled mother cells are usually disposed in an arc in transverse section (figs. 3, 4), although this unity may be broken in places by the interspersion of simple parenchyma-like cells.

The outer parietals are then newly divided parallel to the epidermis, and, of the two layers thus formed, the inner gives rise to a nutritive layer, and the outer, or subepidermal, to an ephemeral middle layer and an endothecium. As many as six cell layers have been observed in the wall of the anther, exclusive of the epidermis. The inner derivatives of the outer parietal give rise to the nutritive layer by anticlinal cell division (fig. 2). The cells of this layer are always uninucleated but may increase in number somewhat as shown by figures 3 and 4. They do not completely enclose the pollen mother cells and are always external to the arc formed by them. These nutritive cells are little differentiated and are very vacuolate during the early stages of microspore formation.

A peculiar sterile tissue may be noted very early in the interior of each antheridial compartment (figs. 2, 3). These parenchyma-like cells occasionally extend entirely across the theca and separate the arc of the microspore mother cells into smaller groups. This ground tissue may be noted in each of the four prominences when the hypodermal cells divide periclinally to form the inner and outer parietals (fig. 1). The primordial pollen mother cells are easily recognized by the time they are no more than two cells removed from the epidermis (fig. 1), are few in number, and, in giving rise to the microspore mother cells, never lose their identity. With subsequent growth and enlargement of the anther, the sporogenous cells form a rather large arc and partially enclose the invading ground tissue which has developed (figs. 3, 4).



FIGS. 1–6. FIG. 1. Transverse section of a portion of a young anther showing inner and outer parietals. ×300. FIG. 2. Transverse section of developing microsporangium. ×300. FIGS. 3–4. The same successively older. ×195. FIG. 5. Pollen grain showing contents. ×500. FIG. 6. Tip end of pollen tube showing sperm nuclei and tube nucleus six hours after pollination. ×500. gc, generative cell; h, hypodermis; ip, inner parietal; mmc, microspore mother cell; op, outer parietal; sn, sperm nuclei; spt, sporogenous tissue; st, sterile tissue; t, tapetum; tn, tube nucleus.

As noted in figure 3, these "internal" sterile cells are very vacuolated, but in later stages they seem to possess much more cytoplasmic material (fig. 4). Their position and orientation, as shown in figures 3 and 4, suggest that they have been instrumental in conducting nutrient material supplied by the anther into the sporangial cavity. As shown in figure 4, they maintain contact with the inner surface of the theca even after the "external" tapetum has broken loose from the sporangia wall. The "external" tapetum absorbs the wall layers of the sporangium and transfers the dissolved nutrient material to the developing pollen grains. Both nutritive layers are then finally absorbed *in situ* by the young microspores.

Two loculi are produced in the anther by disintegration and absorption of the partition between adjacent sporangia. This process begins just beneath that part of the epidermis which is to give rise to the stomium, and proceeds toward the connective. The stomium is formed by a radial elongation of eight or ten epidermal cells on each side of four or five small cells which remain unchanged. The small epidermal cells form a line of weakness along which the versatile anther dehisces longitudinally.

The second mitotic divisions are simultaneous, as is characteristic for the dicotyledons, and a tetrahedral tetrad is produced. Cytokinesis is accomplished by means of the cell plate. The pollen grain is small and has three germ pores. The generative cell is oval, and its nucleus is small in comparison with the tube nucleus (fig. 5). In this condition the pollen grains are shed from the rigorously protandrous stamens.

The style terminates in two large stigmatic lobes which bend backward when receptive. Covering their upper surfaces are large, thin-walled, simple papillae. Immediately beneath the papillate cells, a number of small vascular strands may be observed in transverse section. These veins tend to anastomose as they near the base of the stigma and pass down through the solid style as two separate bundles, one to each carpel. Arriving at the ovarian wall they divide again and give rise to the well developed placental bundles. Each strand traverses the entire length of its corresponding placenta but never extends into the funiculus.

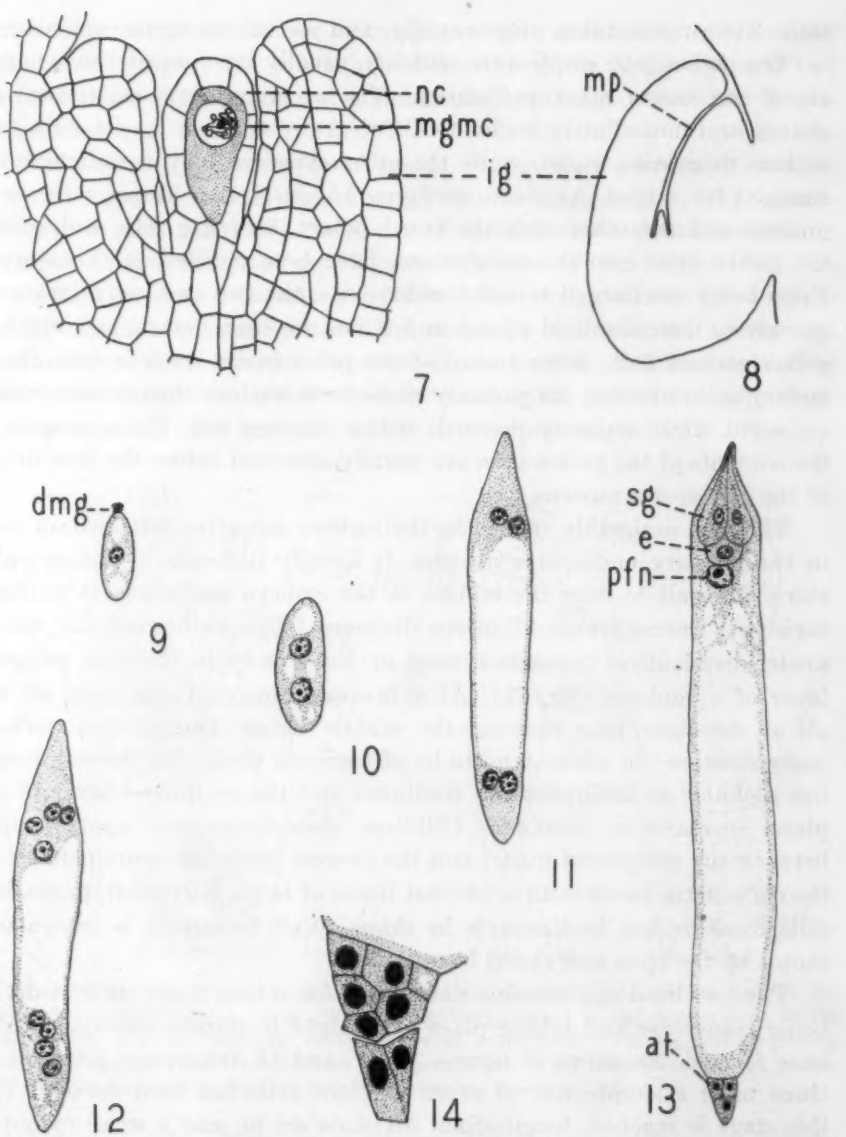
Pollen tubes, coming from monosiphonous pollen grains which germinate on the papillae covered stigmas, penetrate the elongated epidermal cells and soon enter the small vascular strands lying beneath them. Following these veins, the tubes are conducted to the placental bundles from which they emerge at different levels to enter the micropylar canals. Growing out at the surface of the placenta, the pollen tube advances to the nearby micropyle of the anatropous ovule and grows down through the canal to the egg apparatus. While the conduction of the pollen tube is thus endotrophic, for the most part, it becomes ectotrophic in passing over from

the placenta. The pollen tubes grow rather rapidly and usually reach the embryo sac within nine or ten hours after pollination. Figure 6 shows the end of a tube with the two small oval gametes already formed six hours after pollination.

The megagametophyte is of the monosporic *normal type*, involving five successive divisions of the megaspore mother cell before formation of the female gamete. The megaspore mother cell lies immediately beneath the epidermal layer of the nucellus in the central upper portion. It arises directly from a single primary archesporium and is easily distinguished from the other hypodermal cells by its larger size (fig. 7). A single integument is initiated near the base of the ovule at about the same time. This covering reaches the tip of the nucellus during the early prophase of the meiotic divisions (fig. 7) and, growing rapidly, soon extends much beyond its summit, adhering laterally along one side to the wall of the ovary, so that an anatropous ovule is formed. It consists finally of sixteen to eighteen cell layers, and forms a long curved micropyle which opens very close to the placenta (fig. 8).

In both the first and second meiotic divisions of the megaspore mother cell, the spindles lie in a longitudinal direction of the nucellus, and a linear tetrad of potential megaspores is produced. The chalazal spore becomes the functional megaspore while the remaining cells of the tetrad are absorbed. The megaspore, growing considerably, is soon characterized by a centrally located nucleus, surrounded by cytoplasm, and with a large vacuole in each end (fig. 9). Three successive nuclear divisions then ensue, and a normal seven-celled embryo sac is produced in the usual manner (figs. 10, 11, 12, 13). In so doing, the two polar nuclei move along the wall of the elongated megaspore, meet near the center, and fuse before the pollen tube empties its contents into the embryo sac. The large fusion nucleus with its enormous nucleolus then moves back near the egg cell (fig. 13). During the first phase of embryo sac formation, involving vacuolation and the first nuclear division of the megaspore, the epidermal cells of the nucellus covering the megaspore are crushed and absorbed, and the developing embryo sac comes to lie next to the integument.

A slight variation from the normal type of embryo sac formation is often exhibited by the chalazal half where development is somewhat more rapid than that in the micropylar end. The three antipodals may show signs of early disintegration (fig. 13), or there may be an increase in number by the time the embryo sac has matured, followed by disintegration and absorption (fig. 14). These cells are always uninucleated and distinct, but it was not determined whether the increase is due to mitosis or ami-



FIGS. 7–14. FIG. 7. Longitudinal section through portion of ovule showing megaspore mother cell. ×365. FIG. 8. Longitudinal section through young ovule showing integuments and micropyle. ×48. FIG. 9. The functional megaspore showing remains of disintegrating spores. ×365. FIGS. 10–12. Stages in the development of the megagametophyte. ×365. FIG. 13. Longitudinal section of mature embryo sac. ×365. FIG. 14. Longitudinal section of chalazal end of embryo sac showing eight antipodals. ×560. at, antipodals; dmg, degenerating megaspores; e, egg cell; ig, integument; mgmc, megaspore mother cell; mp, micropyle; nc, nucellus; pfn, polar fusion nucleus; sg, synergid.

tosis. The process takes place rapidly, and no mitotic figure was observed.

The pollen tube empties its contents, usually into one of the synergids, about ten hours after pollination. The receiving cell undergoes some change and immediately begins to disintegrate, as shown by its staining reactions to gentian violet, while the other synergid may remain quite unchanged for a time. As shown in figure 15, one sperm unites with the egg nucleus and the other with the fused polars. Starch grains, unloaded by the pollen tube into the embryo sac, have been omitted in this drawing. Upon being discharged into the embryo sac, the two gametes migrate very quickly to their destined places, and it has not been determined which one makes contact first. After fusion of the polar fusion nucleus with the secondary male nucleus, the primary endosperm nucleus thus formed remains quiescent while syngamy proceeds within the egg cell. The synergids and the contents of the pollen tube are usually absorbed before the first division of the endosperm nucleus.

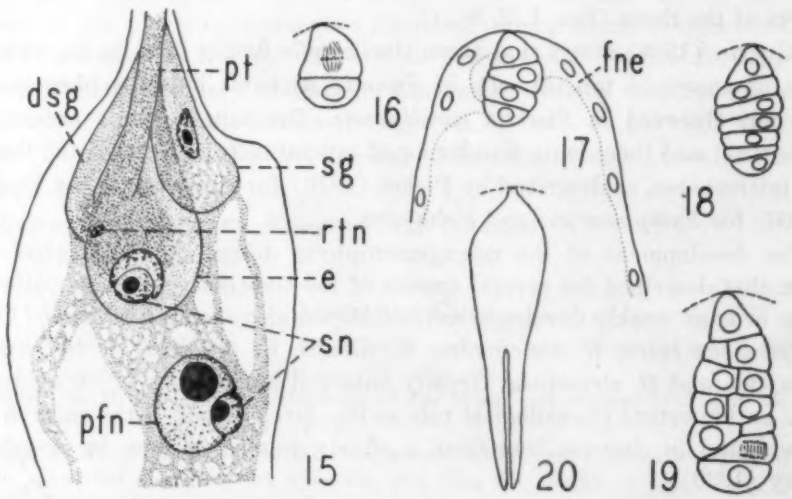
The first noticeable change in the embryo sac after fertilization occurs in the primary endosperm nucleus. It usually descends in the cytoplasm along the wall to near the middle of the embryo sac, where it undergoes division. Successive simultaneous divisions follow rather quickly, the free nuclei distributing themselves more or less evenly in the thin peripheral layer of cytoplasm (fig. 17). At a favorable moment, one may see them all at the same time showing the mitotic figure. During this period of hasty division the nuclei tend to be of fusiform shape, but become more or less globular as multiplication continues and the peripheral layer of cytoplasm increases in thickness. Cellulose membranes then appear rapidly between the peripheral nuclei and the process continues centripetally until the endosperm becomes an organized tissue of large, polygonal, parenchyma cells more or less isodiametric in shape. Wall formation is irregular, as shown by the open and closed boxes.

The fertilized egg remains unicellular for a long time, its first division being transverse and taking place after eight to sixteen endosperm nuclei have formed. As shown in figures 16, 17, and 18, transverse divisions continue until a simple row of seven or eight cells has been formed. When this stage is reached, longitudinal divisions set in, and a small cylindrical body, with blunt free end, is produced (fig. 19). This form is maintained during subsequent development until the cotyledons begin to appear.

The suspensor cells cannot be distinguished during the early stages of embryogeny, but, after the shaft-like body increases somewhat in diameter, seven or eight tiers of cells with four or more cells in each tier are recognized. With further growth, the embryo digests a small amount of the

surrounding endosperm in the micropylar region and finally assumes the form shown in figure 20, consisting of a small terete hypocotyl and two well formed cotyledons. The lower end of the hypocotyl is root and it possesses a small root cap.

Simultaneously with the development of the endosperm and embryo, the embryo sac, as well as the entire ovule, increases in size. The integument, which early manifests symptoms of absorption, is almost completely consumed during the later developmental stages of the ovule. Only the epidermal layer, which becomes the testa of the seed, survives the destruction. By means of continued anticlinal divisions in this layer, a wing two cells thick is formed around the edge of the smooth, flattened seed. The small, terete embryo is imbedded in the micropylar end of the copius endosperm in which food is stored chiefly in the form of protein.



FIGS. 15–20. FIG. 15. Longitudinal section through micropylar end of embryo sac showing double fertilization. ×560. FIGS. 16–19. Early stages in the development of the embryo. ×365. FIG. 20. Matured embryo showing cotyledons. ×48. dsg, disintegrating synergid; e, egg cell; fne, free nuclear endosperm; pfn, polar fusion nucleus; pt, pollen tube; rtn, remains of tube nucleus; sg, synergid; sn, sperm nuclei.

Discussion. As shown in the foregoing, the embryology of *Swertia carolinensis* is essentially like that described by Stolt (1921) for the Gentianaceae. A free nuclear endosperm and three or more weakly developed antipodals are formed. There is no integumental tapetum. A slight variation may be noted in the embryo sac, however, which perhaps more closely resembles the small elongated forms found in the Menyanthaceae.

Microsporogenesis was considered briefly by Stolt (1921) in only two

species. In *Swertia carolinensis*, however, the presence of sterile tissue in the microsporangia is of considerable interest. The occurrence of such tissue is not rare although it has generally been regarded as potentially sporogenous. Campbell (1898), for example, pointed out that in the pollen sacs of certain Naiadaceae some cells do not form pollen. An analogous situation was demonstrated by Bonnet (1911) in several species of the Onagraceae where the pollen sac is divided by partitions of sterile tissue. Guérin (1926) made a similar observation in several species of *Gentiana* and in *Swertia perennis*. In *Swertia carolinensis*, however, this "internal" mass of sterile cells, which functions as a tapetum, evidently does not arise from the inner parietal layer and consequently has no sporogenous potentialities. It is merely a natural "invasion" of the primary ground tissue of the anther into the microsporangial cavity. This phenomenon becomes evident if one follows rather carefully the earlier developmental stages of the theca (figs. 1, 2, 3).

Guérin (1926) states that these sterile cells finally take on the appearance of amoeboid tapetal cells in *Swertia perennis* but this phenomenon was not observed in *Swertia carolinensis*. The tapetal walls persist for some time, and there is no wandering of tapetal cells in between the maturing microspores, as described by Picket (1916) for *Arisaema*, or by Duggar (1900) for *Symplocarpus* and *Peltandra*.

The development of the megagametophyte differs in no essential way from that described for several species of the Gentianaceae. A variation of three or more weakly developed antipodals was also observed by Stolt (1921) in *Gentiana lutea*, *G. asclepiadea*, *G. nivalis*, *G. cruciata*, *G. tibetica*, *G. walujewi*, and *G. straminea*. Greatly enlarged antipodals, which evidently play an important physiological role in the development of the embryo sac, were found in *Swertia longifolia*, a closely related species, by Jacobson-Paley (1920).

The single integument observed in *Swertia carolinensis* is characteristic of the Gentianaceae. And as observed by Guérin (1903) in *Halenia elliptica* and *Gentiana campestris*, it becomes more strongly developed in the micropylar part than at the sides of the nucellus. All but the epidermis is absorbed as the ovule further develops.

Double fertilization was observed although it was not determined which sperm makes contact first. Jacobson-Paley (1920), however, noted that fertilization of either the chalazal polar nucleus or of the fused polars always preceded that of the egg in *Swertia longifolia*.

In the division of the primary endosperm nucleus, the spindle occupies various positions with reference to the long axis of the embryo sac and a free nuclear endosperm, followed by cell wall formation, is developed.

This, and the very small embryo, as pointed out by Schnarf (1931), are both typical for the Gentianaceae.

SUMMARY

1. The embryology of *Swertia carolinensis*, a gentian, is described and compared with that of other species and genera in the family.

2. A nutritive tissue of peculiar origin, apparently sterile, invades the microsporangial cavity and aids the regular tapetum during the development of the microspores.

3. The megagametophyte is of the monosporic *normal type*, involving five successive divisions of the megaspore mother cell before formation of the female gamete. It is much elongated at maturity and often consists of more than three weakly developed antipodals.

4. An integumentary tapetum is not formed although all but the epidermis of the single integument is absorbed during ovule development.

5. Entrance of the pollen tube is porogamous. Double fertilization occurs, and the primary endosperm nucleus so formed remains quiescent while syngamy proceeds within the egg cell.

6. The formation of a free nuclear endosperm always precedes that of embryo development.

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LIGULE-ENDODERMIS OF ISOETES MURICATA VAR. BRAUNII

DOUGLAS W. DUNLOP

Casparian strips and the endodermal like layer at the ligule base of *Isoetes macrospora* Dur. have been described (Dunlop 1949). This finding was of enough interest to cause the writer to investigate and compare the ligule-endodermis of *I. macrospora* with that of another species of *Isoetes* found in Wisconsin.

Material and Methods. Axes of *Isoetes muricata* var. *Braunii* (Dur.) Reed, were collected in Washburn county in about four feet of water from Bass Lake, T–38–N, R–11–W, and killed in Belling's modification of Navashin's fixative. Sections were stained with the crystal-violet-iodine-picric-acid counterstain technique with uniformly good results.

Discussion and Observations. Longitudinal sections of the stem region of *I. muricata* var. *Braunii* showing the development of a series of leaves illustrate the rather rapid early growth of the ligule, (fig. 1A), and show that the ligule-endodermis is differentiated very early in leaf development and represents part of the leaf proper; however, Casparian strips cannot be demonstrated until some time later in leaf development.

The base of each older ligule is ensheathed by a mature endodermis and as in *I. macrospora* each cell of this specialized layer possesses a complete Casparian strip in the four radial walls, (fig. 1B). The Casparian strips are bright blue when stained with crystal-violet and their path about the radial walls is remarkably distinct (fig. 2A). Stained with Sudan IV, the cross sections of the Casparian strips are faintly pink. They are anisotropic when rotated between crossed prisms, this being observed best in lightly stained or unstained preparations.

Vascular tissue associated with the ligule is similar to that in *I. macrospora* both in position and amount. While tracheids do not completely enclose the ligule-endodermis there is a considerable supply distributed throughout the region of the endodermis, and in the plane of the leaf trace this vascular supply reaches all the way around the ligule base from the velum region to the top of the ligule base. In frontal sections of the ligule base the ensheathing distribution of tracheids is probably best seen (fig. 2B). Reticulate tracheids seem to be absent from the vascular sheath of the endodermis although they are found in the trace near by.

Casparian strips of the two Wisconsin species are approximately the same width, ca. 2 μ; however, the two species differ in cell size, nuclear volume, and chromosome number as well as in the sculpture of their meg-

aspore surface. The volume of the endodermal cells of *I. macrospora* is approximately 51 per cent greater than the volume of endodermal cells of *I. muricata* var. *Braunii*. The volume of nuclei of the endodermal layer of *I. macrospora* is approximately 144.0 μ^3 while those of *I. muricata* var. *Braunii* are approximately 73.2 μ^3. This nuclear volume ratio of 2:1 is consistent in the writer's preparations. The diploid chromosome number of *I. muricata* var. *Braunii* is 24–26 and that of *I. macrospora* has been estimated at approximately twice as many (Dunlop 1949).

SUMMARY

1. Casparian strips are present in cells of a specialized layer of the leaf at the ligule base of *Isoetes muricata* var. *Braunii*.

2. The name ligule-endodermis is suggested for this specialized tissue.

3. A considerable supply of tracheids are present at the ligule base and are very closely associated with the endodermis, many of them being in contact with the walls of the endodermal cells.

4. The ligule-endodermis of *I. muricata* var. *Braunii* and *I. macrospora* are alike in structure but differ in nuclear and cell size.

5. The presence of a ligule-endodermis in two species of *Isoetes* indicate the probability of its occurrence in other species of the genus.

6. The location of the ligule-endodermis, its high degree of development, and its association with vascular tissue seem to indicate that it is related functionally to the ligule.

The writer wishes to thank Dr. Eugene S. McDonough and Dr. William N. Steil for critical reading of the note and examination of the preparations.

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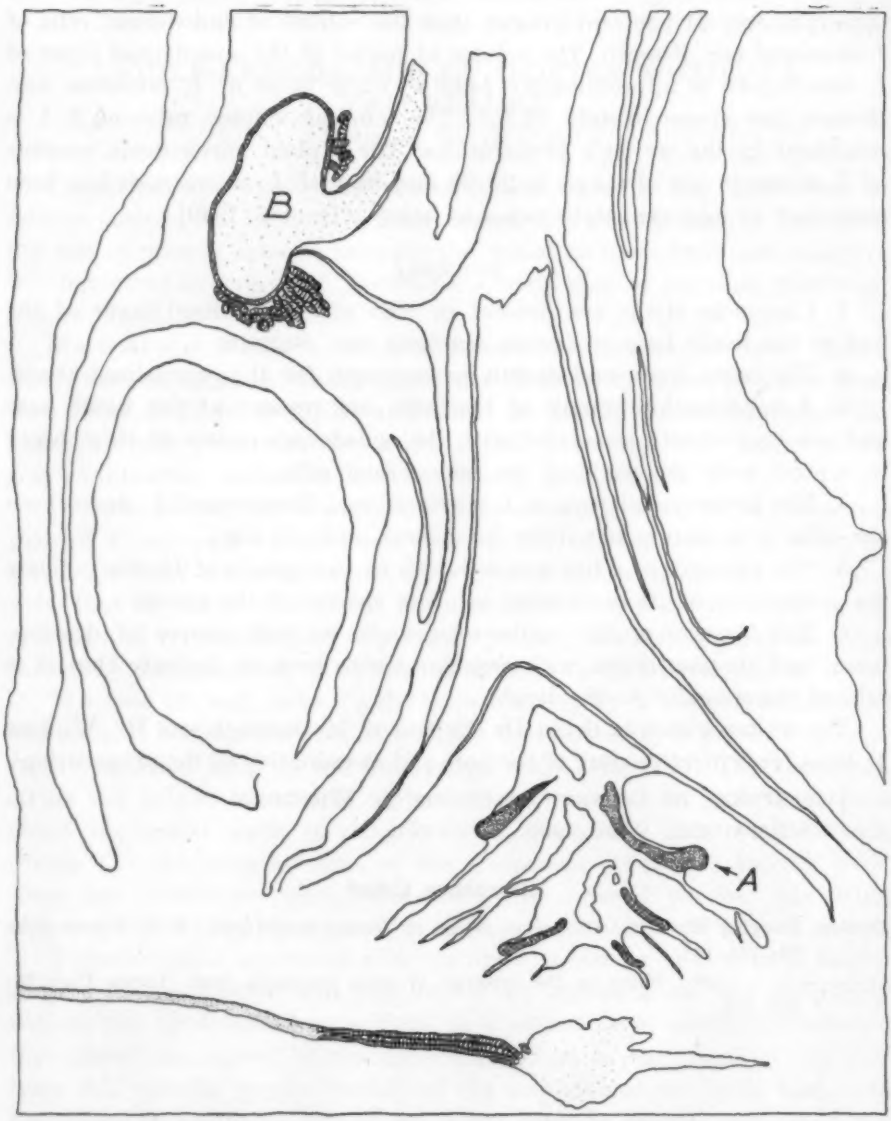

FIG. 1. Longitudinal section of stem tip region of *I. muricata* var. *Braunii*. A. Early development of ligule. B. Older ligule with ligule endodermis and vascular supply.

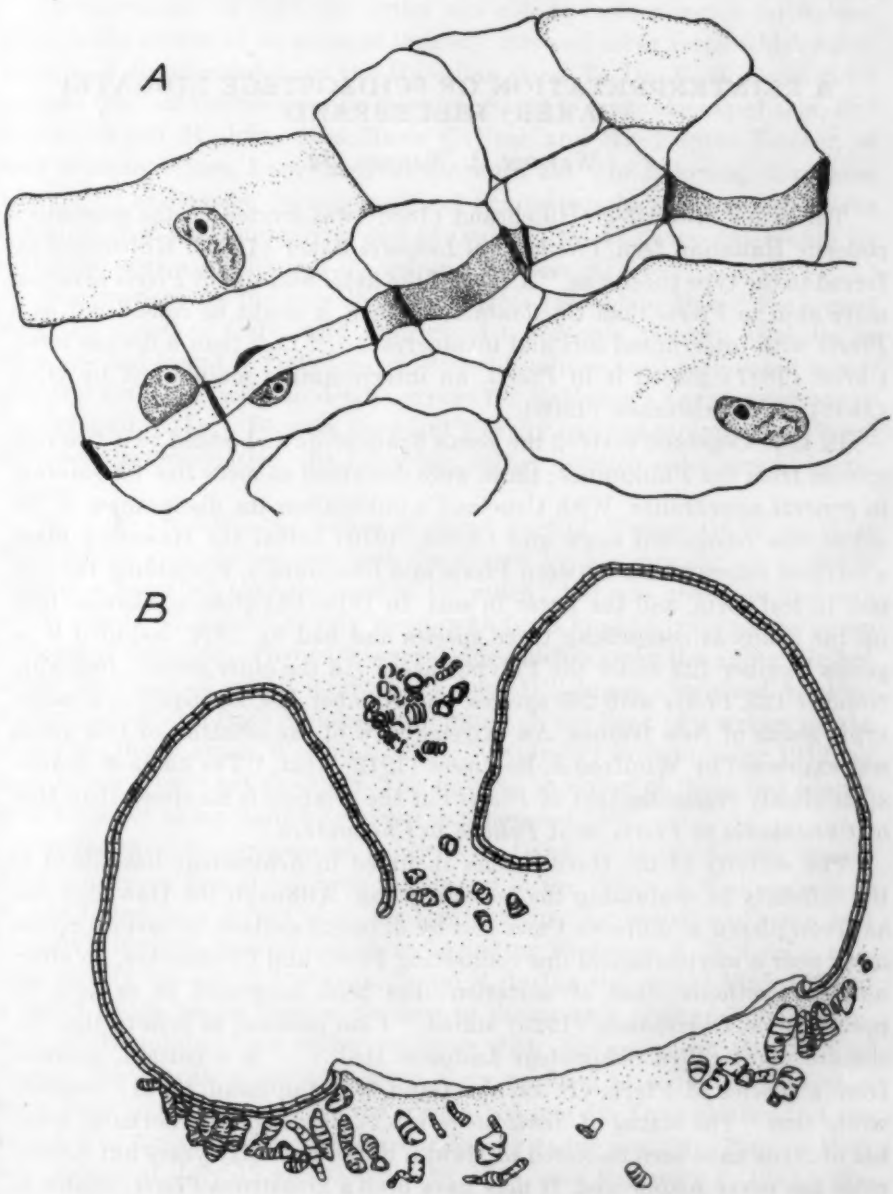

FIG. 2. Ligule-endodermis of *I. muricata* var. *Braunii*. A. Casparian strips in endodermal cells. B. Frontal section of ligule base showing tracheid distribution.

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A REINTERPRETATION OF SCHIZOSTEGE LIDGATEI (BAKER) HILLEBRAND[1]

WARREN H. WAGNER, JR.

The genus *Schizostege* Hillebrand (1888) was erected on the anomalous endemic Hawaiian fern, *Cheilanthes Lidgatei* Baker (1883). Hillebrand referred to the type species as, "A fern of the habit and size of *Pteris biaurita*, more akin to *Pteris* than *Cheilanthes*. In fact, it might be considered as a *Pteris* with interrupted sori and involucres. . . ." Less than a decade later, Christ (1897) placed it in *Pteris*, an interpretation maintained by Diels (1899) and Christensen (1906).

In 1906 Copeland revived the genus *Schizostege* and added to it two new species from the Philippines; these were described as more like *Cheilanthes* in general appearance. With Copeland's publication the distinctness of the genus was recognized anew and Christ (1910) called the Hawaiian plant a striking intermediate between *Pteris* and *Cheilanthes*, resembling the former in leaf-form, and the latter in sori. In 1913, Christensen likewise took up the genus as comprising three species and had by 1934, included it as genus Number 125 under the Polypodiaceae (in the older sense), following Number 123, *Pteris* with 269 species, and Number 124, *Hemipteris*, a monotypic genus of New Guinea. An extreme view of the affinities of this genus was expressed by Winifred J. Robinson (1912), that, "The habit of *Schizostege* closely resembles that of *Pteris* but the relation is no closer than that of *Cheilanthes* to *Pteris* or of *Pellaea* to *Cheilanthes*."

The scarcity of the three species included in *Schizostege* has added to the difficulty in evaluating the generic group. Although the Hawaiian one has been placed at different times and by different authors at various points on or near a morphological line connecting *Pteris* and *Cheilanthes*, an alternative hypothesis—that of mutation—has been suggested to explain its peculiarities. Christensen (1925) stated, "I am inclined to believe that the obscure plant called *Schizostege Lydgatei* Hill. . . . is a mutant, derivate from a species of Pteris (*P. excelsa* Gaud.?)." Copeland (1941) recently wrote that "The status of *Schizostege* is . . . dubious. An enormous number of ferns have been collected in Hawaii in the past fifty years but *Schizostege* has never reappeared. It may have been a monstrous *Pteris*, unable to reproduce itself."

[1] *Lidgatei* was the original spelling of the specific name, but the later authors adopted *Lydgatei*. As his publication on Hawaiian ferns (Lidgate, 1873) also bears this spelling of his name, it is assumed he changed it at some later time, so the first spelling is accepted here.

In the summer of 1947, the writer was able to make a search for *Schizostege* in the course of an attempt to study this and other ferns which seemingly had disappeared from the Hawaiian flora. To Dr. E. B. Copeland I owe the original instruction and encouragement to make the expedition, and to Dr. Harold St. John, Miss Marie C. Neal, and Mr. Eugene Horner, as well as many others, I am thankful for much aid. The following discussion is an effort to describe the occurrence of *Schizostege Lidgatei*, to extend the description of the sporophyte, and to evaluate the evidence concerning its distinctness as a species and the generic problem involved.

Occurrence: As the type locality for this rare plant Baker (l.c.) gave only the island of Oahu, and Hillebrand noted only the two localities at which he had found it. Only two additional localities have been listed subsequently, and these with no details except for Robinson's vague description, "on ground." (l.c.). Because the plant's rarity has had an important bearing on its interpretation, the following, rather detailed notes should be recorded.

On July 18, 1947, the writer explored part of Waihee Gulch in West Maui where this species was first discovered by Hillebrand "in a sterile state at a waterfall near the head of the gulch" but was unable to find any of the plants. This gulch is very steep, with ferns in abundance on the damp bottoms of the slopes. There are several side-gulches along the upper Waihee River, any one of which might have been Hillebrand's original locality. Forbes' specimens from Molokai were found on the bank of a stream on the slopes of Olokui above Waiehu ("Elev. 3000 ft.?") in September 1912, an area which I have not revisited. The stations on either of these two islands have thus not to my knowledge been rediscovered.

Of the three known general localities on Oahu, all in the Koolau Range, I am not aware that it has been recollected in the valley of Wailupe where it was found in a fertile state for the first time by Hillebrand's son and Lidgate. However, several collectors, including Professor A. B. Lyons, one-time science teacher at Punahou, found it during the period 1865–1890 in a valley which has its head at the base of the summit peak of Konahuanui, back of Honolulu. This valley connects with Nuuanu near the head of Pauoa. The plants, a dozen or more, were confined to a limited area on a steep bank immediately above the stream bed, not far from the head of the valley. The stream bed was dry except during rainy weather. (Eugene Horner: letters of July 15 and October 18, 1948, and February 7, 1949.) Mr. Horner visited this station, reported here for the first time, several times in the years 1896–97, and found fertile fronds on each visit. He has kindly permitted me to study this material.

No further collections on Oahu are known until May, 1909, when Forbes, the first botanist of the B. P. Bishop Museum, in the company of the late

C. Montague Cooke, found two plants in the Koolau Mountains between Punuluu and Kaipapau (without numbers on the specimens seen). An additional collection labeled simply "Waiahole Pali, with A. F. Judd, C. M. Cooke, and Porter, Feb. 6, 1912, No. 1746 O[ahu]" was made subsequently. With directions provided by Mr. Cooke, the writer, with Messrs. Charles and Robert St. John, and R. Toupin, made a search on August 31, 1947 for the Punuluu locality, which Mr. Cooke stated was about twenty yards to the left of the continuation of the Castle Trail along the second stream beyond the ridge. As it turned out, this one was not reached, but the first stream, Koluanui Stream, was explored and three large plants were found at the sharp bend about one-half mile downstream from the point at which the trail crosses the stream. At this spot Koluanui Stream is approximately 1750 feet in altitude. The situation in which the plants were growing is a rocky hillside of about 70° slope, and they grew about fifteen feet above the stream, in rich dark humus, pH 4.5 with a LaMotte "Soil Teskit." The three plants were shaded when the sun was overhead, and the *Metrosideros* trees on the mossy slope are abundantly clothed with mosses, indicating rain-forest humidity and rainfall (fig. 1). The fronds are borne erect by the stiff and robust stipes (fig. 3), but the blades, with fullest laminar area exposed to light, are oriented downward parallel to the slope, which is shaded from above. One of these plants was taken for later study. This general area harbors feral pigs which are known to denude hillsides and frequently to root out whole fern-plants. Other ferns growing near-by were *Sphenomeris chusana* (L.) Copel., *Lastrea globulifera* Brack., *Cibotium Chamissoi* Kaulf., *Elaphoglossum reticulatum* (Kaulf.) Gaud., *Dicranopteris linearis* (Burm.) Underw., and *Cyclosorus cyatheoides* (Kaulf.) Farwell. *Sadleria squarrosa* (Gaud.) Maxon, another wet-forest plant, is frequent in the general area.

The difficulty of recognizing this fern in the field should make the following remarks of use to field-botanists. The appearance of this plant was likened by Baker to *Woodwardia radicans,* but Hillebrand compared it to *Pteris biaurita.* As shown in figure 2, the indentation of the veins in the shiny, crisp, living lamina, and the dentations of the fertile margins in these plants with interrupted sori when seen from above, lessen the resemblance of the plant in nature to *P. biaurita* or its local relative, *P. excelsa.* While the latter comparison is doubtless closer phylogenetically, it may not be as helpful as comparison with local ferns less closely related. From a distance young *Cibotium* plants might be confused, but the endemic Hawaiian *Ctenitis honolulensis* (Hook.) Copel. seemed to resemble it much more closely when viewed from a distance of ten or more feet. In general habit and in the dark gray-green color, the appearance is quite similar. Seen closer, however, the *Ctenitis* has various differences which distinguish it.

FIG. 1. Habitat of *Pteris Lidgatei*. Plant in center of picture directly under overhanging moss-covered roots. Koluanui Stream, Koolau Mountains, Oahu, T. H. May 23, 1948. (Robert P. St. John).

FIG. 2. Living frond of *Pteris Lidgatei* with separate sori, showing depression of vein and costules, and shiny, coriaceous lamina. $\frac{1}{4} \times$ natural size. (University of Hawaii).

In the present plant the young living fronds are pale gray-green. The heavily cutinized leaf-surfaces become roughened by depression of the costules and veins. The texture of the living mature pinnae is remarkably thick, and they are brittle. The lobes are broken readily when roughly handled in collecting and pressing. The stout stipes and rachises are dark gray-brown and highly polished. However, the stipes and the long, shiny chestnut-brown scales which invest their bases are hidden by the tangled vegetation of the habitat. Only the flat frond faces can be seen.

All references to this plant indicate its scarcity: Robinson noted an interval of about twenty-five years between Hillebrand's and Forbes' collec-

FIG. 3. Living plant of *Pteris Lidgatei* showing frond habit and thick stipes. 1/10 × natural size. (University of Hawaii).

tions on Oahu, but these were apparently the only ones known to her. Copeland recently (1947) raised the suspicion that it might no longer exist in nature. As the collection described here followed the previous one by 35 years, reasons for the paucity of collections might be asked. An infrequency of occurrence combined with a tendency to grow among numerous mosses and ferns, and its similarity to other, more common genera in casual aspect are probably the factors which make this Hawaiian fern so poorly represented in herbaria. In all likelihood, these factors rather than a chance ori-

gin of the plant by mutation, explain this condition. It is my belief that deliberate search for it on other islands, especially Kauai, would reveal other localities. It should be sought at altitudes between 1000 and 3000 feet, on steep, wooded, fern-covered slopes in wet forest, growing in rich, acid humus above the beds of streams. It is urged, however, that plant collectors observe caution so this endemic fern will be perpetuated; its scarcity, like that of certain other Hawaiian plants, emphasizes that the living, self-reproducing plant in natural occurrences may be many times more useful to future students than abundant packets of parched herbarium mummies.

Description of the sporophyte: Coarse herb, 0.5–1.0 meters tall (fig. 3). Rhizome horizontal, 1.5 cm. thick, 10.0 cm. or more long when mature, solenostelic, the pith 0.5 cm. in diameter, the cortex 0.5 cm. across radially, drying gray-brown (not cream-white as in *Pteris excelsa*). Rhizome bearing about eight green fronds and one or two browned, dead fronds (August), and several remaining stipe bases, the stipes originating very close around the rhizome. Roots extremely numerous, matted, nearly 1 mm. in diameter, 3–15 cm. long, and tapering but little; root-branchlets 0.5 mm. in diameter, borne at intervals of about 1 cm.; the whole root system invested densely with dark red-brown, delicate, straight hairs, 2 mm. long. Stipe bases and rhizome apex clothed with crowded, glabrous, shiny, atrocastaneous paleae, 0.8–1.5 cm. long, 0.1–1.5 mm. broad, linear, gradually narrowing to the attenuate tips of only several cells width. Scale cells elongate, 5–10 times as long as broad, with square or oblique end-walls, the walls dark brown translucent except in the thin-walled cells of similar shape along the margins in one or more layers. Scales remaining several centimeters along stipe but soon falling above this area, leaving remote, tiny black, wart-like spots, 0.5–2.0 mm. in diameter. Fronds, including the stipes, 80 (60–95) cm. long and 40 (20–45) cm. broad, the blades spreading, not dimorphic and usually all fertile. Stipe 45 (25–50) cm. long, 3–6 mm. in diameter, gray-brown, except for lowest several centimeters where it is dark red-brown. Stipe vascular tissue omega-shaped in cross section (as in *Pteris excelsa*). Blade oblong-deltoid to broadly ovate-deltoid, the lamina coriaceous, brittle, dark gray-green (pale gray-green when newly unfolded, and often blotched dark-brown in age). Stomata on lower surface, parallel, the long axes of the openings parallel to the veinlets but avoiding them in an epidermal strip about four times the veinlet width; the pair of guard-cells located distally on more oval and less undulate-walled epidermal cells. Hairs similar to *Eupteris* species on undersurface, remote, with 3 (2) oblong cells, the basal one longest, the apical one with rounded apex and usually tannin-filled. Hairs most frequent in the angles between the costae and costules. Blade bipinnate at base, the basal pinnae provided with 1–4 long basal auricles, the upper pinnae lacking these. Terminal pinna like the lateral pinnae in form, but larger (15–25 cm.), and relatively larger in more immature fronds. All pinnae deeply lobed, becoming less deeply lobed near the apices and in some individuals (as in fig. 6). Rachis not winged with lamina, brownish straw-colored, shiny, sulcate. Lateral pinna-pairs six or less ("8–10" Hillebrand), subopposite, only the basal pair in mature fronds definitely stalked, the stalk

3–4 mm. long, the remaining pinnae usually sessile. Angle of pinnae 70° (60°–80°). Unlobed pinna-tips 3–5 cm. long, broad-caudate. Lowest pinnae 14–27 cm. long, with auricles 12 (2–19) cm. long. Medial pinna-pairs 17 (11–21) cm. long, 5 (4.0–5.5) cm. broad in the middle. Sterile margins of lobes dentate with sinuses up to 0.5 mm. in depth, or occasionally nearly entire, mostly with two veinlet termini per tooth, but at tip only one undivided vein terminus per tooth. Vein plan of lobes pinnate, free (except for

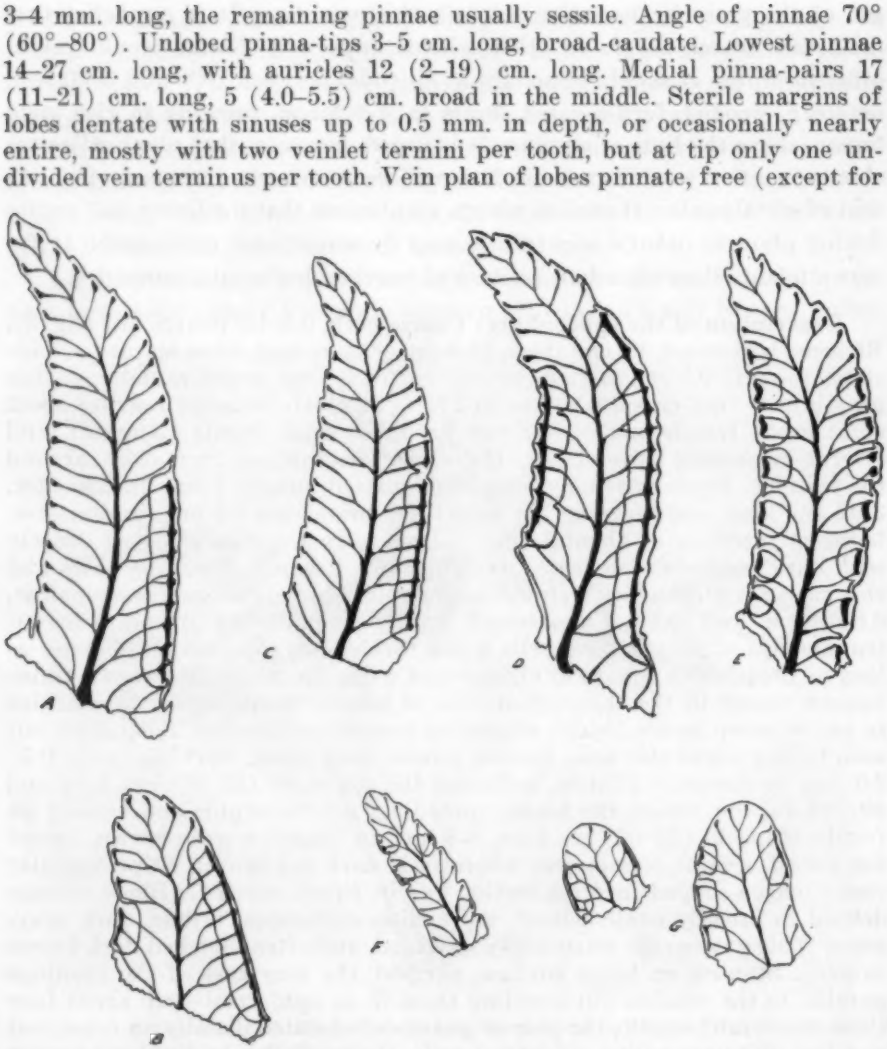


FIG. 4. A–E, *Pteris Lidgatei*. A. *Horner s.n.*, complete coenosorus. B. *Forbes 556Mo.*, complete coenosori. C. *Horner s.n.*, apical interruption of coenosorus. D. *Horner s.n.*, lobulation of indusium. E. *Wagner 5762*, typical discrete sori. F. *Schizostege calocarpa, Copeland 1707*, structure of teeth and sori. G. *Schizostege pachysora, Copeland 1715*, two segments showing the entire margins and sori, and variable anastomoses.

occasional terminal anastomoses as in fig. 4, a). Central lobes with 11 (10–12) mostly once-forked pairs of veins originating along costule; distal lobes with only 2–3 vein-pairs; proximal lobes with 5–18 vein-pairs. Lobes falcate, 10 (9–13) mm. broad, mostly oblong or oblong-triangular, ascending at tips, broadly pointed to nearly obtuse, cut to within 4–1 mm. of the

costa. Lowest vein-pairs along costules of the largest lobes often forked twice, the first furcation next to the costule. Veins and veinlets sunken, and shallowly corrugating the upper laminar surface. Veinlets, including all elongate cells, 120–130 microns in breadth in the middle.

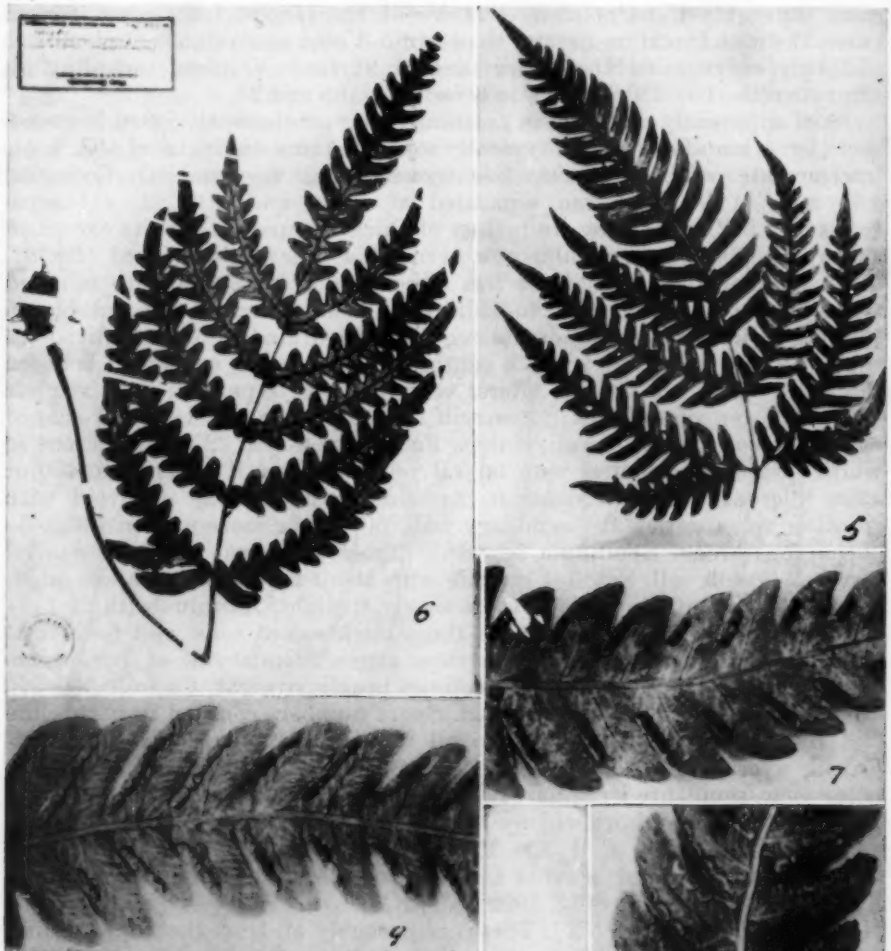
Sori apparently marginal in position, either continuously fused in coenosori (fig. 4, a and b) or more typically separated into distinct sori (fig. 4, e), intermediate conditions being also common (fig. 4, c and d). Coenosori 4.31 mm. in length, often separated at distal ends (fig. 4, c); separate sori 1.5–2.5 mm. long. Indusium of thick texture, dull white except in age when it becomes irregularly or evenly blackish tannin-stained (fig. 8), a broad, entire flap, a more or less lobed flap, or separated into rounded triangular or square discrete indusia, 1.5–2.5 mm. long, 1.5–2.0 mm. broad. Receptacle likewise continuous to regularly separated into equal divisions, subtended correspondingly by a continuous connecting cross-vein between the upcurved termini of the lateral veinlets, or by separated cross-veinlets between sister veinlet tips; cross-vein near tip often reduced to T-shaped expansions of simple lateral veinlets. Fertile cross-vein 325–375 microns in width except at junctures with lateral veinlets where it expands to 400 or more microns. Fertile cross-vein tracheids mostly oblong or ovoid with spiral or spiral-reticulate secondary wall, 50–150 or more microns long, 5–35 microns broad. Sporangia crowded, numerous, large; stalk of two cell layers, 3–5 cells tall. Sides of capsule with about fifteen more or less quadrangular thin-walled cells, the walls nearly straight. Annulus with 21 (17–22) thickened cells; stomium with three thick-walled cells, and four thin-walled cells below these, and two or three above. Stomial side of sporangium less convex than opposite side, sometimes nearly straight. Capsule 500–560 microns tall, 415–530 microns broad. Spore numbers counted in herbarium material 51–55, probably 64 when all formed and present. Spores tetrahedral, averaging 57–81 microns, trilete, rarely bilateral, triangular in polar view, sculpture irregular, rather crowded with warts of various sizes, tetrad scar distinct, bordered by ridges, and occasionally not reaching the angles (Selling, 1946, p. 51, figs. 111–118; Brown 1931, fig. 15f).

Material examined: *Forbes s.n.* Koolauloa Mts. between Punahuu and Kaipaupau, Oahu, May 8–13, 1909 (NY, BM); July 8, 1909 (US); Punahou Mts., Oahu, May, 1909 (NY). These are probably all from the same locality. All specimens show separate sori.

Forbes 1746 O[ahu]. Waiahole Pali, with A. F. Judd, C. M. Cooke, and Porter, February 6, 1912 (BM). Separate sori.

Hillebrand and Lydgate s.n. Schizopteris Lydgatei Hbr., Cheilanthes Baker, Flora Hawaiiensis, collected by Dr. William Hillebrand and J. M. Lydgate, Ex Herbarium J. M. Lydgate (BM); Schizopteris Lydgatei, Oahu, Hillebrand, The New York Botanical Garden, Herbarium of Lucien M. Underwood (NY). These fragments are probably from Wailupe, Oahu.

Horner s.n. Base of the summit peak of Konahuanui, Koolau Range, Oahu, 1896–97 (Horner Herbarium and UC). These comprise two apical pinnae, one frond tip with apical pinna, and three lateral pinnae, two middle fragments, two herbarium sheets including the specimen illustrated in figure 5, and a blade or blade apex with a large terminal pinna and one pair of laterals. All specimens are coenosoral with a tendency to separate sori.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Wagner 5762. Koluanui Stream, Hauula Forest Reserve, Koolau Range, Oahu, August 31, 1947 (UC). Specimens all with distinct sori.

Forbes 556 Mo[*lokai*]. Slopes of Olokui, above Waiehu, elev. 3000 ft.? September, 1912 (BM). A young frond with rhizome, coenosoral (fig. 6).

Additional illustrations: Baker, 1886, Pl. 1635, figs. 1–4: figures 1 and 2 illustrate an irregular tendency for coalescence of sori in a pinna, and a pinnule intermediate between those with coenosori and those with entirely separate sori. Figures 3 and 4 illustrate the sorus. Christ, 1910, fig. 106: A whole young frond, apparently with fusion of sori, and the apex of another, showing discrete sori. Robinson, 1912, Pl. 41: An apical portion of a frond with three pairs of lateral pinnae and discrete sori, and a large basal pinna with two auricles is illustrated.

Relationships: As shown in the foregoing description and figures, some of the materials of the plant currently called *Schizostege Lidgatei* lack completely the characteristic interruption of sori, the original basis for generic separation. Of the few localities known, specimens from two—Konahuanui, Oahu, and Olokui, Molokai—have typical pteroid coenosori. While all the specimens seen from the more northerly localities in the Koolau Range have entirely separate sori, those of Hillebrand's from Wailupe Valley, Oahu, show occasional tendencies toward coenosoral fusion. The Maui plants found by Hillebrand were sterile. In view of the collections with coenosori, and the various conformities of this plant with known elements in *Pteris* to be discussed below, the proposal is made that it be reinterpreted as *Pteris Lidgatei* (Baker) Christ, and that name will be used here.

Pointing out that difficulty in distinguishing and evaluating species is characteristic of the Hawaiian flora, Copeland (1947) remarked that "*Schizostege* is dubious as a single species." Christensen, more than a score of years earlier, had speculated that this plant might be a mutant of *Pteris excelsa*. Yet, having seen living plants of both of these entities in their native habitats and having examined them comparatively in the herbarium, I cannot endorse the latter suggestions. On the contrary, *P. excelsa* differs from its supposed offshoot not only in lacking the marked tendency for regular soral division—a "schizostegeoid tendency"—but also by its occurrence in different habitats, its narrower fronds, basal pinnae which have but one auricle or none, the usually much thinner laminar texture and paler color,

FIGS. 5–10. FIG. 5. Frond with coenosori, Konahuanui, Oahu, T. H. *Eugene Horner* (Horner Herbarium) ¼ × natural size. FIG. 6. Young frond with coenosori and unusually blunt lobes, Olokui, Molokai, T. H., *C. B. Forbes 556 Mo.* (B. P. Bishop Museum) ¼ × natural size. FIG. 7. Pinna with coenosori, *Horner s.n.* (University of California) natural size. FIG. 8. Pinna tip with coenosori and undulate indusia, showing tendency for black tannin accumulation in old indusia, *Horner s.n.* (University of California) Natural size. FIG. 9. Pinna with deeply lobed indusia, *Horner s.n.* (University of California) Natural size. FIG. 10. Pinna with typical separate sori, *Wagner 5762* (University of California) Natural size.

narrower and longer segments, finer serration of the margins, more compound and closer venation, narrower and more fragile indusium, smaller and differing spores and sporangia, and various other features. That *P. Lidgatei* is a mutant in the conventional genetical sense, of *P. excelsa* is obviously doubtful; that so many apparently unrelated characters would mutate simultaneously seems very unlikely. The constant differences of *P. Lidgatei* from any other known fern would appear to make its specific status unquestionable.

Although the plant under consideration was first described in *Cheilanthes,* and Copeland (1906) regarded the Philippine ferns he placed with it as approaching *Cheilanthes,* a sound concept of immediate affinity between *Schizostege* or *Pteris* and *Cheilanthes* has not been developed by any author. On the other hand, Bower (1928) regarded *Pteris* as a derivative from dicksonioid ferns with marginal, bi-indusiate sori, and *Cheilanthes* as probably descended from schizaeaceous ancestors, never more than uni-indusiate from the beginning. He stated that, "To us who now realize that a very similar soral structure may arise along distinct phyletic lines, the habit characters acquire additional value in these comparisons." Remarking that the habit of *Hypolepis* is different from the group of *Cheilanthes,* he considered *Dennstaedtia* and *Hypolepsis,* themselves with indusiate ancestors, as likely prototypes for both the davallioid and pteroid ferns. Exindusiate osmundaceous and schizaeaceous types were his supposed ancestors of his gymnogrammoid forms, including *Cheilanthes,* through ferns in which the uni-indusiate condition had arisen by the "phyletic slide" of marginal sporangia and subsequent modification of the leaf-tissue of the margin as an indusium.

This viewpoint of the origin of *Cheilanthes* is not shared by most authors, and Christensen (1938) related his "Gymnogrammeoideae" to the "Pteridoideae." Copeland (1947) revived the possibility that *Cheilanthes* (including *Notholaena*) may be derived from or related to *Hypolepis,* noting a species of the latter genus similar to *Cheilanthes* in habit. He states that *Cheilanthes* has conspicuous characters in common with the "Pterideae." Neither of these hypotheses, it should be noted, places *Pteris* and *Cheilanthes* in direct line with each other in evolution. Although the immediate relationship of the Hawaiian *Schizostege* can be deduced with a fair degree of assurance, this cannot be said for the Philippine plants. Their morphology must be studied comparatively, however, before valid grounds can be established for interpreting them as possible phylogenetic links between pteroid and cheilanthoid ferns.

The Hawaiian fern appears actually to be an isolated insular derivative of the group of *Pteris quadriaurita* Retzius, which evolved perhaps in an ancient Hawaiian flora and is comparable to such unique local species of

large genera as *Microsorium spectrum* (Kaulf.) Copel. and *Athyrium Macraei* (H. & G.) Copel. The group of *P. quadriaurita* in the strict sense comprises many species, some of which are very similar. Hieronymus (1914), restricts this pantropic group to all species of *Eupteris* with pinnate leaf-blades, more or less deeply divided lateral pinnae, and of which the lowest pair or pairs bear one to three (very rarely more) basal auricles. In all of them there is a terminal pinna similar to but mostly larger than the upper lateral pinnae. The venation is free and the lateral veins of the lobes are mostly forked, only several of the apical ones being simple. The lowest lateral veins almost always end above the sinuses between the lobes. This definition of Hieronymus is perhaps too strict; other obviously closely related elements, such as *P. biaurita* L., with veinlets anastomosing along the costae, and probably even more different forms should be included if this is to represent a natural section of the genus. Hillebrand's comparison of *P. Lidgatei* to *P. biaurita* referred to the habit of the plant, but in the type of venation the present plant agrees with *P. quadriaurita*. The veinlets are thicker and more remote than usual. The hairs of this fern agree in form with those of other allegedly glabrous *Eupteris* species. Although surely distinct from it, the nearest fern in Hawaii to *P. Lidgatei* is *P. excelsa*, which Hillebrand (1888) called, "The largest species of the quadriaurita group." These *Pteris* species, as well as the Litobrochia section and other groups, bear small spines or elongate pointed flaps at the costule bases on the wings of the costae. As such appendages appear to be absent in the section *Lonchitis* and the groups of *Pteris cretica* and *P. longifolia*, this character is of importance in assessing affinities within the genus, as had been shown as early as 1839, in the enumeration of *Pteris* species by Agardh. The differences of the Philippine plants in all of these characters will be discussed below.

The unique division of the submarginal line of sporangia into separate groups to form individual "involucres" each with its own receptacle, fertile cross-vein, and indusial flap has been the one and only real distinction of the Hawaiian *Schizostege* from *Pteris*. The schizostegeoid condition of separate sori, however, should not be considered primitive to the pteroid coenosorus. Bower's placement of such types as *Paesia*, *Pteridium*, and *Histiopteris*—all with coenosori—as hypothetical analogues of ancestors of *Pteris*, supports this conclusion. The schizostegeoid sorus is more probably a modification of the usual Pteris sorus.

Even if there were not coenosoral specimens, the fact that *Schizostege* was originally distinguished by its regularly broken line of sori does not mean that this distinction in itself is necessarily of valid generic value. Diversity in this respect, but without generic division because of it, is seen is such pteridaceous genera as *Adiantum* and *Lindsaea*. The coenosoral con-

dition is found in such examples as *Adiantum lucidum* (Cav.) Sw. and *Lindsaea ensifolia* Sw., and discrete soral arrangements in *Adiantum obliquum* Willd. and *Lindsaea Macraeana* (H. & A.) Copel. Although such analogies have certain weaknesses, it should be noted again that the existence of strikingly parallel modifications in different fern families has led to the evaluation of soral structure, in numerous instances, as being of less and less critical significance in fern systematics. A convenient example of radically different sori in plants of close affinity is the modification seen in a single previously mentioned Hawaiian endemic, *Athyrium Macraei*. Here occur both typical dorsal athyrioid sori and sori terminal on vein extensions beyond the leaf-margins. Individuals with the latter type were formerly referred to an artificial genus, *Deparia*, in which were placed two unrelated elements, similar only in the sori. Apparently a similar state of affairs obtains in the genus *Schizostege*.

In *Pteris*, some species of the section *Lonchitis* (upheld by some authors as generically distinct) regularly show abbreviated sori located in the sinuses and separated by the sterile, distal lobe-margins. Mr. C. A. Weatherby (in a letter) called to my attention the fact that the "West African *Pteris pteridioides* (Hook.) Ballard (*P. brevisora* Baker) has such short sori that Hooker originally described it as a *Hypolepis*." It is interesting also to note that Christ (1897) placed this plant closest to the Hawaiian one. *Pteris* species of other sections show a tendency toward interruption of coenosori as indicated by Sprau (1933). The same tendency may be seen readily in young or incompletely fertile examples of *P. excelsa* in Hawaii (e.g. *Wagner 5251*, Haleakala, Maui). Thus the abbreviation or interruption of coenosori is not unusual in *Pteris*.

The breakage of coenosori observed regularly in fully mature *P. Lidgatei* appears to depend on characters of the margins. Diels' use (l.c.) of the serrate or toothed margin of the sterile segments as a character for distinguishing this plant from the *P. quadriaurita* group does not cover the situation. Various species of the group possess toothed sterile margins, these almost always with fine, one-nerved teeth, at least near the apices of the segments. Diels' other criteria, segment and pinna pointing and complexity of the blades, likewise do not hold. The teeth of sterile margins of *P. Lidgatei* serve not so much to separate it from other *Pteris* species as to explain the schizostegeoid sorus, which seems to depend on the spatial relationship of the bottoms of the sinuses to the line of sporangia. Such a conclusion differs from that of Hillebrand, who considered "the interruption not occasioned by a lobulation of the segment" (op. cit. p. 632), where he was presumably thinking of pinna margins of the Lonchitis type. The present interpretation stresses the form of the margins, the formation of indentations being reflected in the development of separate sori.

Toothed sterile margins in *Pteris* generally show from one veinlet-terminus to a tooth (dentate, with one veinlet per tooth) to two veinlet-termini to a tooth. In the latter condition the proximal veinlet is reflected by a marginal bulge or small point, the distal one serving a more conspicuous, longer point (essentially bidentate), or the proximal one shows no marginal bulge (dentate or crenate, with two veinlet-termini per tooth). In sterile margins of *P. Lidgatei* most of the teeth away from the segment tips belong to the latter category, and the two sterile veinlet branch-endings are nearly on a line with, or beyond, the sinuses. Since, as it is generally agreed, the pteroid indusium is "false," i.e., results from continued outgrowth of the margin beyond superficial sporangial initials (Bower, 1928), the schizostegeoid indusia appear to be homologues of these teeth. The two veinlet-termini present are evidently joined in the typical pteroid manner by the characteristic mass of specialized short tracheids subtending the receptacle. When indusia of herbarium specimens are dissected away from the thick, reflexed tissue of the leaf-margin, the folded-over margin in coenosoral specimens appears as a continuous band of tissue; but in specimens with discrete sori there remain instead tooth-like inward projections of the margins separated by sinuses, which correspond in position with those of the distal sterile margin. If this assumption is correct, an ontogenetic study might be expected to show that in development the line of sporangial initials is nearly congruent with, or beyond, an imaginary line connecting the sinuses of the developing leaf where the schizostegeoid sorus type is formed; the sporangial line would consequently be interrupted by the sinuses. Further growth could therefore result only in scalloped, infolded indusial segments, these in some cases overlapping laterally. As the size of teeth and dissection of coenosori do not appear to be correlated, the various soral conditions must be due to differences in the time of appearance of sporangial initials and sinuses. This and the related problem of factors connected with the origin of sporangial initials and its bearing on formation of commissural tracheid masses and indusia could be especially well studied in the present species because of the large size of the structures involved, and the presence of both separate sori and coenosori in the same species.[3] The distal portions of the lobes have simpler veins and deeper teeth. It is here that coenosoral fronds

[3] Parallel division of coenosori by toothed margins, dentate with two veinlets per tooth (in this case usually somewhat closer to bidentate), in which the larger sinuses are in line with sori is to be seen in a specimen of *P. dentata* Forsk., *U.C. 398432*. Here sporangial production is pronounced in the lower halves of the segment margins, and in these lower parts typical coenosori are found. But acropetally there is a transition to the sterile and toothed condition of the margin by breaking up of the coenosorus, and individual sori here are schizostegeoid, served by two veinlets and separated by acute sinuses. P. *tremula* R. Br. specimens, e.g. *U.S. 61265*, *U.C. 61264*, and *U.C. 42965*, show a similar condition.

most often show occasional discrete sori (fig. 4, c). On strongly soriferous plants the sori extend relatively closer to the tips. These, like the distal teeth of sterile lobes, are served by only one veinlet, modified terminally by the "T-shaped" type of receptacular vein described by Hillebrand.

The type of segment described here showing pteroid coenosori with continuous fertile veins subtending the uninterrupted receptacles would be expected to form sporangial initials prior to marginal sinuses in ontogeny, so that such sinuses fail to appear and the indusium then develops as an entire flap. Intermediate development is seen in those examples where the indusium is continuous at the base, but lobed along its free margin, as in some of the sori on the fragments illustrated by Baker (1886) and some of Horner's specimens (fig. 4, d). Hillebrand, with the material available to him, had not seen complete junction take place in the intra-marginal veinlet even when several sori coalesced. This imperfectly connected condition of the fertile vein may likewise be considered intermediate between typical schizostegeoid plants and the material described here. It may be that only fully mature leaves express the marginal condition believed responsible for complete coenosoral separation. Forbes' Molokai specimen, the small frond illustrated by Christ (1910), and the Horner material are evidently all more or less juvenile and possess more or less uninterrupted coenosori. Further field study or, even better, observation of cultivated plants grown from spores, is needed.

In addition to the inclination toward regular coenosoral interruption, this species is notable for the exceedingly thick texture of the lamina and indusium, especially in old dark-blotched fronds. Such a texture is, however, not unknown in *Pteris*, as is shown by the Andean *P. coriacea* Desv. (e.g. *U. C. 679440*). Individual specimens of other species in the quadriaurita group, which more closely resemble the present plant, also show similarly thick and rigid textures, e.g. *P. arguta* Ait. (*U. C. 205101* and *U. C. 203282*), and a specimen of *P. excelsa* from Kwantung, China (*U. C. 611422*). Among other Hawaiian "pteridophytes" also, there are conspicuous tendencies in certain genera toward coriaceousness. Thus the two local species of *Psilotum*, the two native *Ophioglossum* species, and the one *Vittaria*, contrast with their nearest relatives to the south and west in thickness of branch or frond. The texture of *P. Lidgatei*, then, is not unique in the genus, and is paralleled by textures in certain other Hawaiian plants (perhaps evolved by similar selective factors?). Although it is not as large in overall dimensions as many species of *Pteris*, the thickness of lamina, large spores and sporangia, stout stipes, heavy veins broadly spaced, large scales, and wide, tough indusia bespeak its general robustness.

The two other ferns placed in *Schizostege* were collected in April, 1905,

along a creek at San Ramon, District of Zamboanga, Mindanao, Philippine Islands, by Copeland. *Schizostege pachysora* was found at about 2500 feet altitude, and *S. calocarpa*, with the more divided fronds, was found further upstream at about 3000 feet. Neither has been recollected in this locality nor found elsewhere. Of them, Copeland (1947) recently wrote, "Whether they are really congeneric with that of Hawaii or merely fit the fairly detailed generic diagnosis remains questionable."

The most obvious differences between the Hawaiian species and the two Philippine ones are vegetative. Unlike the type species, the frond structure in both of the other plants (cf. Copeland 1906, Pl. 12; Christ 1910, fig. 107) is clearly different from the quadriaurita group of *Pteris*, as Copeland has already indicated (1947), and cannot be matched in other sections of that genus. But close similarities between the two Philippine plants themselves show that they are congeneric, and share various features precluding obvious relationship to *P. Lidgatei*. The smaller fronds (40–65 cm. tall) of the Philippine plants are conspicuously narrower in outline, and the apex is formed by gradual reduction in symmetry, rather than by a single, marked, apical pinna. The rachises are scaly and dull and so strongly winged that only about one to three of the narrow pinna-pairs in the simpler species and six to nine in the more dissected are really free. The rest of the pinnae merge into the wings. Neither has segment margins like *P. Lidgatei*, as will be discussed further. The spine-like free or appressed appendages along the ventral surfaces of the costae at the segment bases, found in many *Pteris* species including *P. Lidgatei*, are absent in the Philippine plants. Vein anastomoses in the lamina in *Schizostege pachysora* contrast sharply with the Hawaiian plant, but *S. calocarpa* possesses mostly free veins, probably consequent upon greater dissection. Both of the latter species have a fleshy and thicker texture when alive but when dry are papyraceous, instead of brittle-coriaceous, and are much more hairy, especially on the axes, than *Pteris Lidgatei*.

Resemblance between the sori of the Philippine and Hawaiian plants seems at first sight considerable, but a careful comparison with excellent materials of the latter, which were unavailable when the Philippine plants were first described, shows that this is probably coincidental. Such a mode of coenosoral separation as suggested for *P. Lidgatei* cannot be seen here because *Schizostege pachysora* has margins which are perfectly entire, and *S. calocarpa* has much broader teeth of a different form than those of the Hawaiian plant. Discrete sori in the last are served regularly by two veinlet termini (apically by one), while in *S. pachysora* there is variation from one to five veinlets terminating in an individual sorus, and in *S. calocarpa* the sori are served mostly by only one veinlet-terminus. The very broad

serrations of *S. calocarpa* show from one to four veinlet-termini, but only one (occasionally two) ends in a sorus (fig. 4,f). There may thus be half or more of the tooth margin sterile, and as the sorus in these cases is proximal on the tooth, it is the distal pointed portion of the tooth which is free. Consequently, in these ferns the "schizostegeoid" condition must have come about by some different course.

In the absence of manifest affinities to known elements in *Pteris*, it is possible that *Schizostege pachysora* and *S. calocarpa* may together merit separation from that genus. It would be desirable, however, to await more collections and further study before erecting a new genus. Christ seems to have come to consider the Hawaiian plant as separate from *Pteris* only after he had seen the two Philippine plants with apparently identical sori. It is evident, however, that these similarities in sori are only superficial. It may be concluded, then, that a genus defined by this doubtful character and embracing two elements with widely different fronds—only one of these with known close prototypes in *Pteris*—is artificial.

SUMMARY

The genus *Schizostege* Hillebrand was based on *Cheilanthes Lidgatei* Baker, an anomalous Hawaiian fern originally considered to differ from *Pteris* in having interrupted sori. Two Philippine plants with apparently similar sori were placed with it. All three are rare and poorly known ferns, and the Hawaiian had been suggested to be a possible mutant of *Pteris excelsa* Gaud. A rediscovery of this plant in 1947 showed that it occurred on steep wooded slopes in wet forest, growing in acid humus above a stream. An examination of hitherto unstudied material indicates that it should be reinterpreted as *Pteris Lidgatei* (Baker) Christ. Specimens from two of the six known localities possess uninterrupted pteroid coenosori with continuous fertile veinlets. The characteristics of the plant are so marked that it is undoubtedly a distinct species, but any close relationship with the genus *Cheilanthes* is questionable. In general features, especially frond habit, type of venation, and appendages of the costae, it conforms with the quadriaurita group of *Pteris*. Since short sori are found in certain *Pteris* species as a mature state or as a transient juvenile form, and since such pteridaceous genera as *Adiantum* and *Lindsaea* contain species with coenosori and species with discrete sori, this by itself does not appear to be a natural generic criterion in this case. It is suggested that the separate sori found in typical *P. Lidgatei* may be due to the formation of the margins of the lobes, involving a growth correlation between the establishment of the sinuses of the teeth and the development of the sporangial initials. The thick leaf-texture is not unique in *Pteris*. The two Philippine plants, mutually

closely related, placed with the Hawaiian plant, differ from it and the *P. quadriaurita* group in the habit of the frond with the terminal pinna formed by gradual reduction in symmetry and the winged rachis, the segment margins, indument, absence of costal appendages, venation, and texture. Soral similarities are probably due to convergent evolution and do not provide evidence of affinity. A genus comprising these two dissimilar elements is therefore considered artificial.

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TORREYA

PROCEEDINGS OF THE CLUB

Minutes of the Meeting of May 3, 1949. The meeting was opened at 8: 05 P.M. by President Matzke at Columbia University; 30 members and friends were present. The minutes of the preceding meeting were read and approved.

Dr. Berthe Delaporte of the Institut Pasteur, Paris, presented a paper on "The Structure of Bacteria." Her abstract follows:

A great many observations have been published about the structure of Bacteria, without any one receiving general acceptance. Recently, however, there has been such close agreement among the observations of different studies using new methods of staining—either after acid hydrolysis (Feulgen, Giemsa) or after enzymatic digestion—that it now seems probable that we are arriving at a knowledge of the true structure of bacterial cells in many species.

Only the simultaneous use of many different methods of observation (on living cells without staining; with vital staining; with staining of metachromatic corpuscles, lipids, glycogen, and nuclear substance) can enable us to form a concept of the structure of bacterial cells.

The cells of most bacterial species have metachromatic corpuscles and lipid globules; in addition to these, certain species also have some glycogen, and others (sulfur bacteria) have sulfur globules. In every bacterial cell there is also a nuclear element, containing—as do the cell nuclei of every plant and animal species—desoxyribonucleic acid. This element divides at the moment of cellular division, before the formation of the transverse membrane, and has many characteristics of a nucleus. Nevertheless, its intimate structure is not sufficiently well known to permit us, at present, to identify it as a true nucleus.

The shape of the nuclear element depends on the shape of the cell. It is a spherical mass in cocci, a central ovoid mass in ovoid cells, a roundish granule in very short rods, and an elongated body, situated lengthwise of the cell, in long rods (axial thread). When reserve substances (lipids, glygen, metachromatic, sulfur, etc.) are found in the central part of the cell, they push against the nuclear element and deform it, and can also fragment it into several parts.

Division of the nuclear element takes place by simple stretching and separation into two identical parts, without any special internal structure being apparent. A granule lengthens, takes on a dumbbell shape, and then divides into two granules, which pull away from each other. An axial thread separates in the middle into two parts. A small rod, transverse to the long axis of the cell, divides lengthwise into two parts, which move away from each other in the direction of the long axis of the cell.

When a new culture is made, the cells soon enter a stage of very active multiplication, during which the nuclear elements divide more rapidly than the transverse membranes are formed. This results in cells that have two or four nuclear elements, sometimes more. In rods, each of the potential cells, consisting of one nuclear element with its surrounding cytoplasm, is usually

very short and approximately square; the nuclear element in these cells takes the form either of a compact mass or of a short transverse rod compressed between the adjacent substances. When the rhythm of divisions slows down, the cells have time to elongate between nuclear divisions and the nuclear element gradually resumes the shape typical of the species.

The spore of *Bacillus* species develops, in the beginning, from a fragment of nuclear substance, which surrounds itself with a homogeneous cytoplasm. This prespore grows slowly to the size of a normal spore, becoming ovoid in shape, with a nuclear element in the form of a short rod. This nuclear element migrates to the periphery of the sporal cytoplasm, often taking (for example, in *B. cereus*) a ring shape, most commonly seen in side view as a curved rod with slightly thickened extremities. In the course of this change the sporal cytoplasm alters its staining affinities and the spore becomes enclosed in a refractive membrane. During spore formation there is a progressive—not always total—disappearance of the nuclear substance and protoplasm that were in the sporangium, outside the spore. The spore is then liberated.

At germination, the spore swells while the nuclear element comes into the center, enlarges, undergoes various transformations, and then divides At about this time the young rod emerges from the spore. Often two or three divisions of the nuclear element are completed before the first transverse membrane is visible. When the resting spore remains inside the remnant of the sporangium membrane, it is sometimes possible to see that at germination one or two granules of chromatic substances are discarded on the exterior surface of the spore coat; these granules are probably remnants of the nuclear substance of the sporangium, outside the spore.

After discussion the meeting adjourned at 9: 05.

Minutes of the Meeting of May 17, 1949. The meeting was opened at Hunter College, with President Matzke in the chair, at 8: 25 P.M.; 25 members and friends were present. The minutes of the preceding meeting were read and approved.

The following names were presented for membership in the Club: Sustaining Member: Kent H. McKnight, Provo, Utah; Active Members: Margery S. Anthony, Ann Arbor, Michigan; Earlene Atchison, Chapel Hill, North Carolina; Ernest Ball, Raleigh, North Carolina; John L. Blum, Buffalo, N. Y.; Paul R. Desjardins, Berkeley, California; James G. Dickson, Madison, Wisconsin; Beatrice B. Exner, Baton Rouge, Louisiana; A. Alfred Foster, Farmingdale, N. Y.; Luis E. Gregory, Turrialba, Costa Rica; H. J. E. Hardh, Tikkurila, Finland; Gunnar W. Harling, Stockholm, Sweden; Benedict A. Hall, Cortland, N. Y.; J. R. Holbert, Bloomington, Ind.; Thomas D. Howe, Defiance, Ohio; Beatrice Krauss, Honolulu, Hawaii; Lucien Levesque, Montreal, Canada; Karl Maramorosch, Brooklyn, N. Y.; Margaretha G. Mes, Pretoria, South Africa; John H. Mullahy, Mobile, Alabama; C. L. Porter, Laramie, Wyoming; Howard C. Reynolds, New York, N. Y.; Bruno Schusnig, Igls, Austria; Nils E. Svedelius, Uppsala, Sweden; Ida Werner, New York, N. Y.; Hugh Wilcox, Corvallis, Oregon; John J. Wurdack, New York, N. Y.; Justin Zender, Lawrenceburg, Indiana; Joseph G. Zoril, Fort Collins, Colorado; Associate Members: Nellie Allen, Manasquam, New Jersey; Hope Mathewson, New York, N. Y.; Jane Meyer, Yonkers, N. Y.; Mrs. R. E. Noble, Brooklyn, N. Y.; Henri Prat, Montreal, Canada; A. H. Sparrow, Upton, N. Y.; Prof. Van Iterson, Baarn, Netherlands; Clara Weigele, Trenton, N. J. All were elected.

Dr. Harold W. Rickett of the New York Botanical Garden addressed the Club on

"Travels of John Bradbury up the Missouri River in 1801 and 1811." His abstract follows:

> John Bradbury (1768–1823) is known chiefly for certain specimens collected on the Missouri River in 1811, which served as the basis of new species described by Pursh in his *Flora*. These specimens are in the Academy of Natural Sciences of Philadelphia. Most of Bradbury's extant specimens, however, are preserved in the Public Museum of Liverpool, from which city Bradbury was sent out to America. These, with a packet of letters from or concerning Bradbury, it was the speaker's privilege to examine during the summer of 1948. Bradbury also published a book, *Travels in the Interior of America*, after his return to England in 1816. This contained a vivid account of the journey up the Missouri, of the vegetation and nature of the country, of various adventures with skunks, bears, and Indians; experiences which are confirmed and enlarged by some of the letters written from America. The letters also explain much that was hitherto unknown about the later history of the specimens, and explain how Pursh came by some of them. They also make clear just how Bradbury failed to realize the success which he anticipated; it was largely a matter of money, which both he and his sponsors had under-estimated. Impoverished by the expenses of his expedition, having lost many of the specimens gathered at such pains, Bradbury resigned from the service of the Liverpool Botanical Garden, and went to New York where he engaged (unsuccessfully) in business for several years. He returned to England only to find that Pursh had reaped the scientific reward of his collections; and finally returned to America with his family, first to St. Louis, later to Middletown, Kentucky, where he died only a few years later.

The meeting was adjourned at 9:25, and refreshments were served by members of the Hunter College botanical staff.

Respectfully submitted,

DONALD P. ROGERS,
Recording Secretary

FIELD TRIP REPORTS

May 1. Netcong, N. J. Amid lowering skies and scattered showers, three carloads of dauntless souls gathered at the Netcong, N. J. railroad station Sunday morning May 1. Because of the fear that the heavens might open at any moment, the group adjourned to Maj. Barry's residences (several cottages and bungalows, including his new 4-story skyscraper designed to place the owner on a level with various species of bird life and afford a vista of woods and Budd Lake). Lunch was enjoyed in the rustic log cabin "Cotswold." Having decided that the rain might hold off a few hours, the group hiked up the Fire Tower for a view of rolling woodlands and too many nimbus clouds. Thence a brief trip to a blueberry swamp where we found the usual skunk cabbage, anemones, and other spring flowers, as well as a number of mosses. At this point the rain fell, Bill (ye hound dog) turned tail and streaked for a dry home, followed by most of the group, except for a few hardy souls who dug specimens amidst a warm spring downpour. An hour later the group was back at Cotswold in cozy chairs playing "Twenty Questions" 'till the rain should stop. The skies lightened somewhat and the three cars of flower lovers went by back roads to Waterloo. Enroute several stops were made to see cowslips (marsh marigolds), early ferns and a variety of other plants, as well as the shiny red leaves of young poison ivy. At Waterloo, the group inspected the ruins of the old Morris Canal locks of the vintage of 1800, and surveyed the inclined plane up which towboats filled with anthracite from Pennsylvania mines once journeyed to Jersey City. The hour

being late, the group adjourned to drive homewards, sorry that the weather had not permitted more time on flower study, but grateful that despite the showery day, there had been a chance to get together and enjoy some of the pleasures of seeing early flowers and opening green buds. Attendance: 10. Leader: Maj. Lyman F. Barry.

May 1. Silver Lake, White Plains, N. Y. A goodly number of plants were observed but nothing out of the ordinary. The most observable feature was the very great lack of birds, there being fewer than at any time Miss Wiley could remember. Attendance: 6. Leader: Farida A. Wiley.

May 1. Serpentine Barrens, Chester Co., Pa. The weather was showery in the A.M. Two of the largest and best known barrens in the country were visited. These outcrops of serpentine support a restricted but quite interesting flora. First stop was made at Unionville barrens located about eight miles southwest of West Chester. This barren is noted for its spectacular display of moss pink (*Phlox subulata*) and serpentine chickweed (*Cerastium arvense oblongifolium*). Despite the fact that the season was about two weeks ahead of normal, both the phlox and chickweed were in fine flower giving the area the appearance of being solidly covered with a pink and white carpet. Other plants observed in abundance here include *Senecio Smallii*, *Arenaria stricta* (both with abundant buds but not in flower), *Antennaria neodioica* (in flower) and *Saxifraga virginiensis* (in flower and fruit).

In the P. M. the group drove southward to the Nottingham barrens about five miles below Oxford, Pa., and near the Maryland border. This barren is quite different from the Unionville barrens in that it supports an arborescent growth, pitch pine (*pinus rigida*), post oak (*Quercus stellata*), black-jack oak (*Q. marilandica*) all developing into fair sized trees. Also thickets of *Smilax rotundifolia* and various shrubs densely cover the area. Along the outer edge of the barrens were found the following: *Cerastium arvense oblongifolium* (in flower), *Arenaria stricta*, *Antennaria plantaginifolia* (in flower), *A. neglecta* (fruit fully mature), *Sisyrinchium mucronatum* (in flower), *Salix tristis* and *S. humilis* (both in fruit). Attendance: 7. Leader, Louis E. Hand.

May 1. Van Cortlandt Park, N. Y. Despite the threatening weather, the early time, and the several other Torrey Club trips scheduled for this date, the group set out for early flowering plants and migrating birds. Of the birds, 32 species were noted but apparently there had been no real migration during the night as very few warblers were seen. A great deal of the Van Cortlandt Park area is being dug up for roads and extension of the golf course, but the flowers were plentiful, as expected. A good stand of bluets (*Houstonia coerulea*) seem to be spreading in one section of the old nursery grounds which is interesting as this common plant is rare in Manhattan and Bronx. On a hill overlooking a public golf course, extensive stands of dutchman's breeches were noted. This hill holds most of the early flowering spring plants in rather large numbers: the common toothwort (*Dentaria laciniata*), early saxifrage (*Saxifraga virginiensis*). A few years ago the hill was covered with *Hepatica triloba* but this had disappeared, probably through picking. Nothing rare was seen and the trip ended as the rain began about twelve noon. Attendance: 4. Leader: William Rissanen.

May 14–15. Camp Thendara on Lake Tiorati, Palisades Interstate Park, N .Y. The New York Section of the Green Mountain Club was pleased to have a larger number of Torrey Botanical Club members than usual with them for their annual Bird Census at Camp Thendara on Lake Tiorati. The weather was perfect in every way, except for a short-lasting thunderstorm late Saturday afternoon. Neither species nor individual birds recorded came up to the number listed for last year. This seems to have been a condition reported from several other places as well. Vegetation was much farther advanced than has been usual for this census time. Hence, there was good botanizing for those who wished to study plants when no thrilling bird observation demanded attention. Beautiful vistas with lakes and mountains, both on the way to camp and from the spacious porch overlooking Tiorati, combined with abundant food served from the busy kitchen within the camp, made time pass all too quickly. This was pervaded by a friendly atmosphere of mutual interests and good fellowship and enhanced by the presence of our bird guide,

Mr. Howard H. Cleaves, noted lecturer and traveler, with his wealth of out-of-door experiences, which he generously shared with the group. This annual week-end outing of the Torrey Botanical Club and the New York Section of the Green Mountain Club is an event of long standing. May it continue to be an occasion looked forward to with pleasant anticipation in the years to come. Attendance: 15 Torrey members and guests. Leader: Laura Woodward Abbott.

May 15. Terrace Pond, N. J. The high point of the trip was a plentiful stand of a hepatic, *Riccardia multifida*, in fruit. At least it was *R. multifida* last fall. At this time of year it might be *R. palmata!* This was the first time any of us had seen the species in fruit and the leader was the only one present who had seen the species at all. We may describe it as fairly scarce hereabouts since all of us had been working on the hepatica for years. The leader was also able to show a lichen, *Arthonia gregaria*, in the only station known to him in northern New Jersey. Attendance: 4. Leader: G. G. Nearing.

May 15. Shawangunk Mountain, N. Y. Nature was very kind for this trip, in marked contrast to last year. Mr. Crabtree was under the weather, but his daughter pinched-hit for him. The *Rhodora* was in perfect form and several new stands were found. That and *Arenaria groenlandica* made the trip well worth while. There was an abundance of *Cypripedium acaule*. Leader: J. A. Crabtree.

May 15. Forked River, N. J. This was the seventh Torrey trip in the last decade to this splendid location and each visit has produced many new plants. Eighteen new species and one variety were observed on this trip. These additions along with four species and one variety reported by Hollis Koster, from collections made on former trips and just recently identified, make a grand total of 479 species. Localities visited on this trip were (1) thickets, open areas and meadows of State Game Farm and (2) Middle Branch bog and along railroad south of it. Among the new species seen on the trip was *Arisaema pusillum* (Peck) Nash. Some authorities make this small "Jack" a variety, form, or subspecies of *A. triphyllum*. It does however bloom several weeks later than the latter and grows in bogs. The colony of *Listera australis* discovered on the Club trip of June 21–22, 1947 has now increased to some two dozen or more thriving specimens, which were in full anthesis on this date. Also admired by the group were two plants of *Arethusa bulbosa* in full flower and of a strikingly deep pink hue. This is early for the fully developed specimens of this orchid. Attendance: 11. Leader: Louis E. Hand.

May 29. Middletown, N. J. We were too late for the bloom of *Pogonia verticillata* but saw many plants in fruit. The stand is healthy and appears to be spreading. The abundance of beech and the finding of several plants of *Orchis spectabilis* made this woodland seem more like north Jersey woods than like the coastal strip which extends southward. Attendance: 9. Guest leaders: Mrs. Martha Taylor and Mrs. Ruth Doremus.

June 4. Morris Arboretum, Philadelphia, Pa. A goodly crowd gathered at the Morris Arboretum where they were welcomed and botanically entertained by Dr. Schramm and Mr. Skinner. The herbarium was extremely interesting as were the trees of foreign origin —cedars, etc. Attendance: 25. Leaders: Dr. J. R. Schramm and Mr. Henry T. Skinner.

June 5. Richmond, Staten Island, N. Y. This date is a little early for the more interesting plants which can be seen in the sandy fields and salt marshes of this region. The dry conditions prevailing on the hillsides did not help matters any. In the marsh behind a church, a large stand of the false indigo, *Amorpha fruticosa*, was in full flower. There must be over fifty large shrubs of this plant growing well in a rather compact group. This stand is believed to have been planted by Mr. William T. Davis some years ago. Another plant which was noted growing abundantly in the same region and on the hillsides was alfala, *Medicago sativa*. It was conspicuous because of its unusual size, the majority of the plants being over or approaching a yard in height. A rare plant seen along the road was *Cerastium arvense* var. *oblongifolium*, growing in areas having serpentine rock such as this region has. Attendance: 9. Leader: William Rissanen.

June 5. Oswego River, N. J. The canoe trip was held as planned and thanks to everybody concerned, Miss Williams, Hack's Canoe Retreat, and the perfect weather, it was

even better than the previous one. We stayed our departure for some time waiting for a car which got lost. The length of the trip and the short time prevented the botanizing we would like to have done. Though who could have missed the continuous stand of southern white cedar on either bank of the stream or the broad expanse of Martha bog and the higher and dry pine forest in the background? Only two canoes were upset and that caused nothing but a slight wetting. It was arranged to have cars at each end of the trip so there was no paddling up stream. Attendance: about 20: Leader: Marion Williams.

June 12. Elysian Lodge to Sunfish Pond, Warren Co., N. J. This was the second Club trip over this route; the initial trip being August 10, 1941. The weather was clear and very hot. From the Elysian Club, group followed abandoned Kaiser Road to the ridge crest and thence southward, along the Appalachian Trail, to Sunfish Pond. Return by same route; round trip distance, six and one half miles. A brook parallels Kaiser Road for a short distance at the start and some northern plants were seen there, including *Acer pennsylvanicum, Betula lutea, Rhododendron maximum, Viola rotundifolia,* etc. Farther along Kaiser Road but below the ridge crest *Arabis canadensis, Scrophularia leporella, Galium lanceolatum, Panicum Boscii, Castilleja coccinea,* and other plants were found in flower. In addition to plants, the advance members of the party surprised a red fox, which quickly took to the underbrush. On the A. T. proper, nine new species were added to the trail list for this section. Best find was a colony of paper birch (*Betula alba papyrifera*) at Tock Swamp. On the previous trip this was passed by for *B. populifolia* on account of the dark "stained" bark which gave it an unnatural appearance. The characteristic ovate leaves however quickly revealed its identity this time. Two plants of *Rhodora* (past flowering) were found and a number of plants of *Cornus canadensis* were still in flower. A short distance along the trail a small red spruce was seen with more and larger specimens back in the swamp. Also off the Trail, a small colony of *Coptis trifolia* was seen in fruit. Due to heat haze, the usual spectacular distant views from the various exposed sections of ridge were not obtained. Attendance: 17. Leader: Louis E. Hand.

June 19. Watchung Reservation, N. J. This trip was for the purpose of determining the hepatic flora in the Watchung Reservation in Union Coutny, N. J., as the Union County Park Commission is preparing a list of all plants and animals found within the Reservation. Dr. H. N. Moldenke of the New York Botanical Garden is in charge of the botanical survey and specimens collected on this trip will be sent to him. In a visit to this region last summer the leader had found a large stand of *Metzgeria conjugata* in a cool ravine, and we found it still plentiful on the sides of the moist cliffs on this trip. A better find was *Lejeunea cavifolia,* a not too common plant. This specimen does not answer to the type as described in Frye & Clark's HEPATICAE OF NORTH AMERICA, but seems to be intermediate between the type and its variety *planiuscula,* lacking the numerous oil cells required in the type but having larger underleaves than elsewhere in the park. The other liverworts collected or seen were: *Lophocolea heterophylla, Anthoceros laeris, Pellia epiphylla, Calypogeia trichomanis, Cephalozia bicuspidata, Plectocolea hyalina, Odontoschisma denudatum.* In the afternoon the members came to the Museum in the Park and discovered that Mrs. Gladys P. Anderson, a member of the Torrey Club, was to give a talk on the flower families. So we joined their meeting. Attendance: 9. Leader: William Rissanen.

June 26. Allaire, N. J. Due to the heat and distance only six reported for the trip and very little was done in the way of botanizing. As yet the State has done nothing to develop the park though they do have a caretaker. The list of plants is growing slowly. Attendance: 6. Leader: V. L. Frazee.

INDEX TO AMERICAN BOTANICAL LITERATURE

COMPILED BY

LAZELLA SCHWARTEN
WITH THE COLLABORATION OF THE EDITORS OF THE TAXONOMIC INDEX

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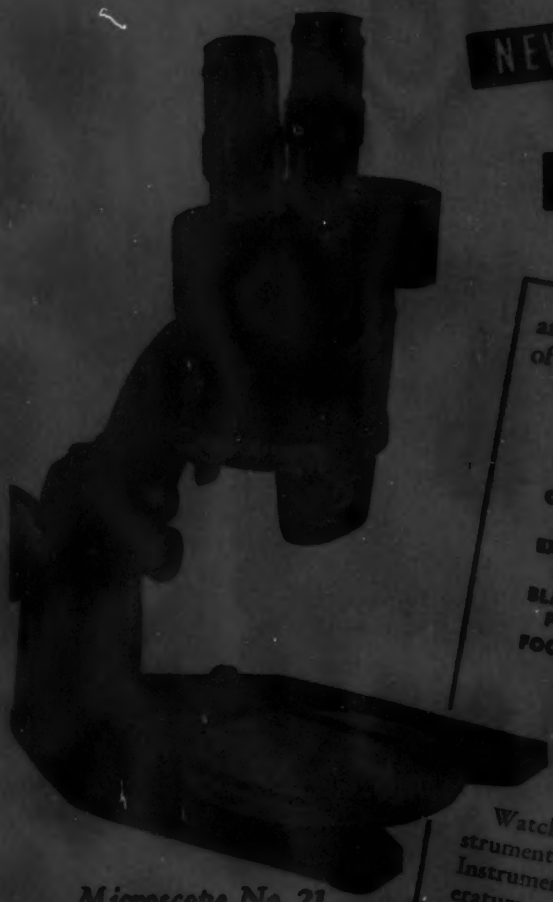

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